# The effectiveness of Table Mountain National Park Marine Protected Area in the conservation of rocky shore biodiversity

By

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# General abstract

Establishment of marine protected areas (MPAs) has intensified in recent years, and there are now over 6800 MPAs worldwide. However, there is a prominent need to assess their effectiveness in terms of protecting biodiversity. In Chapter 1, I provide the theoretical background to this dissertation and define its central goal, i.e., to assess the effectiveness of no-take ('restricted') sections of the Table Mountain National Park MPA (TMNP MPA), relative to zones that are designated as 'controlled', where harvesting can take place under national regulations.

Chapter 2 compares the effectiveness of no-take versus harvested areas in the TMNP MPA in protecting the biodiversity of intertidal rocky shores. Surveys were conducted to compare (1) the densities and sizes of exploited species and rarely harvested species, and (2) community composition, between these two levels of protection. Some clear patterns emerged. Firstly, no-take areas had significantly greater densities of the commonly harvested limpets *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei*, most obviously on sandstone ledges where abundances were greatest. In contrast, densities of the rarely harvested limpets, *S. cochlear*, *S. longicosta* and *S. granularis* did not differ in a manner reflecting protection levels. Secondly, *C. granatina* and *S. argenvillei* were significantly larger in no-take areas, although *C. oculus* displayed the opposite pattern. None of the rarely harvested limpets showed differences in sizes between protection levels. Thirdly, community composition differed significantly between protection levels. No-take areas were characterised by a greater abundance of commonly harvested limpets and mussels, while harvested areas were dominated by ephemeral and corticated algae, due to their release from grazing pressure by limpets.

Chapter 3 focuses on a subset of the sites, all lying on the west coast and all comprising sandstone rocks. First, in a temporal comparison, I evaluated changes in densities and sizes of limpets and in community composition between historical data from 1970 and my sampling in 2017, at two sites where harvesting has intensified since 1970. This analysis showed three kinds of changes: (1) the appearance of alien species; (2) the effects of increased harvesting; and (3) the direct and indirect effects of these changes on other species. Secondly, to disentangle the effects of harvesting from those of alien invasions, I made spatial comparisons using my 2017 data, between two harvested sites and two sites in a no-take zone. One striking result was

transformation of mid-shore zones by the appearance of the invasive Mediterranean mussel *Mytilus galloprovincialis*, and the indirect effects of this on the demography of the granular limpet *Scutellastra granularis*. Adults of this limpet have been excluded by the mussel, whereas juveniles find a secondary home on the shells of the mussel. In addition, harvesting has decimated the granite limpet *Cymbula granatina* and Argenville's limpet *Scutellastra argenvillei*. This has led to the proliferation of opportunistic seaweeds, such as *Ulva* spp., or corticated algae, notably *Pachymenia orbitosa*. The dual effects of alien invasive species and over-harvesting thus have major ecosystem effects.

In chapter 4, densities of the limpet *Cymbula granatina* were manipulated at two sites within a fully-protected no-take area to generate four density levels ranging from zero to maximum natural densities, to evaluate the effects of harvesting this limpet on the community composition. Following removal or substantial thinning of *C. granatina*, community composition changed, cover of corticated and ephemeral algae increased and recruitment of *C. granatina* decreased. These outcomes were, however, dependent on the time frame considered, as algae underwent an annual cycle, and the effects of limpet removal were evident only during cooler months when the algae proliferated. All these effects have management implications.

Chapter 5 provides an overview of the findings from this dissertation and their management implications. The major limitation of the dissertation is that interpretation of results was clouded by an absence of reliable data on actual harvesting rates as reflected in the numbers and activities of people operating in the restricted and controlled portions of the MPA, and of the efficiency with which law enforcement takes place. Nevertheless, strong evidence emerged that no-take areas within the MPA are effective means of conserving biodiversity, and the effects of harvesting deduced in Chapter 2 and 3 were verified by the experiment undertaken in Chapter 4, in which depletion of a dominant and commonly harvested limpet, *Cymbula granatina*, did yield algal proliferations like those evident in harvested portions of the park. The fact that this outcome was observed only at certain times of the year points to the need for studies and monitoring to be undertaken over sufficient time scales to produce meaningful results.

# Chapter 1: General introduction

Efforts to establish marine protected areas (MPAs) as a tool to conserve marine biodiversity have intensified worldwide, to the extent that over 6800 MPAs exist worldwide (Babcock et al. 1999, Benedetti-Cecchi et al. 2003a, Laurel & Bradbury 2006, García-Charton et al. 2008, Kirkman 2013, Bennett & Dearden 2014, Costello 2014, Abecasis et al. 2015, Coppa et al. 2015, Costello & Ballantine 2015, Xu 2015, Horta et al. 2016, Dehens & Fanning 2018). In South Africa, 19 MPAs have been proclaimed on the coast, as of 2000 (Chadwick et al. 2014); and an additional 21 Offshore Marine Protected Areas that were proposed (Sink 2016) were gazetted in 2019, bringing the total area inside MPAs up to 5% of the Exclusive Economic Zone. As a result of growing numbers of MPAs, questions have been asked regarding their efficacy in mitigating anthropogenic impacts and allowing recovery of populations (Benedetti-Cecchi et al. 2003a, García-Charton et al. 2008, Abecasis et al. 2015, Coppa et al. 2015, Dehens & Fanning 2018). This topic has received much attention worldwide. In South Africa, critical examination of the performance of MPAs has often focussed on particular species rather than entire communities. Specific reserves that have received attention include Langebaan Lagoon in the West Coast National Park (Kerwath et al. 2009, Hedger et al. 2010), Dwesa-Cwebe Nature Reserve (Lasiak 1993a, b, 1998, 2006, Branch & Odendaal 2003, Nakin et al. 2012, Nakin & McQuaid 2014, 2016), Tsitsikamma (Buxton & Smale 1989, Buxton 1993, Cowley et al. 2002, Brouwer et al. 2003, Branch & Odendaal 2003), de Hoop (Bennett & Attwood 1991, 1993, Attwood & Bennett 1994, 1995), Goukamma (Götz et al. 2008, 2009a, b, Kerwath et al. 2008, 2013), Pondoland (Maggs et al. 2013, Mann et al. 2016) and Maputaland (Currie et al. 2012, Floros et al. 2012, 2013, Nel et al. 2013).

Relatively little attention has been paid to the Table Mountain National Park (TMNP), although Lechanteur (1999) and Lechanteur & Griffiths (2002) did demonstrate that reef fish were more abundant in the Castle Rocks Reserve section than outside, despite this reserve being quite small. Such evaluations, as well as similar comparative assessments of entire communities, are important for the adaptive management of MPAs which aims to improve their performance. As managing authorities are increasingly moving to an ecosystem-based approach for the management of fisheries (Crowder & Norse 2008), they rely on scientific evidence from community-level surveys to implement suitable and relevant measures (Benedetti-Cecchi et al. 2003a, García-Charton et al. 2008, Abecasis et al. 2015, Coppa et al. 2015).

To ensure appropriate monitoring and evaluation of MPA performance, several criteria have been developed to evaluate MPA effectiveness with regards to protecting biodiversity (Hockey & Branch 1997, Alder et al. 2002, Roberts et al. 2003a, Himes 2007). Firstly, the effectiveness of MPAs can be assessed by comparing the biomass, densities and size distributions of organisms and the composition of communities inside and outside MPAs (Durán & Castilla 1989, Lasiak 1998, Branch & Odendaal 2003, Fraschetti et al. 2005a, Parnell et al. 2005, Nakin et al. 2012, Nakin & McQuaid 2014). This approach is based on the premise that an MPA reduces overexploitation, protects spawner biomass and supplements recruitment of stocks (Attwood et al. 1997, Hockey & Branch 1997, Roberts 2005). In this context, comparisons are often made between different localities with different levels of protection, to establish whether specific regulations are helping to achieve the targets set for MPAs. Secondly, effectiveness can be assessed by comparing the current densities and size distributions of both exploited and rarely exploited species in non-exploited and exploited areas with historical data from these areas prior to MPA declaration (Anderson et al. 2009, Nakin et al. 2012, Nakin & McQuaid 2014). The rationale is that exploited species would be expected to show differences, whereas non-exploited species are less likely to differ between harvested and protected areas.

Ideally, a sampling programme should combine both before vs. after the establishment of an MPA with comparisons of control vs. impacted areas in what is a termed a BACI (Before-After-Control-Impact) design. This is not always possible where baseline data are lacking, but provides the best opportunity to evaluate whether populations have increased or decreased in density or body size after the establishment of an MPA, compared to previously recorded densities and body sizes (Parnell et al. 2005, Parravicini et al. 2013) inside and outside the MPA. A case study from California showed that although densities of many invertebrate species such as lobsters, abalone and octopus were high in both non-exploited and exploited areas, only densities of sea urchins increased when MPAs were declared (Parnell et al. 2005). In South Africa, historical data have proved essential in identifying effective MPAs for the conservation of seaweeds based on presence/absence data (Anderson et al. 2009). For assessment to be impactful, it is also desirable to quantify the magnitude of threats such as harvesting outside and inside MPAs to determine the potential of MPAs to reduce such effects (Zupan et al. 2018). These approaches emphasise the need for historical data when assessing MPA effectiveness, and the frequent lack of historical data has been highlighted as a challenge for the evaluation of the efficacy of MPAs (Fraschetti et al. 2005a).

Apart from protecting biodiversity inside their boundaries, MPAs provide benefits that may extend beyond their boundaries, such as water purification, enhancement of fisheries by emigration of adults, and the supply of larvae to adjacent exploited areas (Roberts et al. 2001, 2003b, 2005, Roberts 2005, Keller et al. 2009, Cole et al. 2011, Alexander & Gladstone 2012, Kerwath et al. 2013). In this way, they provide economic and social benefits through improvement in water quality and the productivity of fishery resources (Alder et al. 2002, Himes 2007). In addition, MPAs are used as reference points to evaluate effects of disturbance on species, populations and communities (Lasiak 1993a, 1998, 1999, Lasiak & Field 1995, Branch & Odendaal 2003, Cole et al. 2011, Nakin et al. 2012, Nakin & McQuaid 2014, 2016). However, these benefits may not be realised if implementation of legislation and compliance remain low and hinder performance of the MPAs (Coppa et al. 2012, 2015, Nakin & McQuaid 2014). Furthermore, the design of MPAs and their connectivity within larger-scale MPA networks also plays a role in determining their effectiveness.

In this regard, several criteria have been established to allow assessment of the effectiveness of MPAs (Emanuel et al. 1992, Hockey & Branch 1997, Roberts et al. 2003a, b, Blamey & Branch 2009, Foster et al. 2017). These include the need to establish MPA networks that cover the full range of biogeographic regions, habitats and species, with the aim of ensuring representative protection of all habitats and species within each biogeographic region, or ecoregion, as differences in species composition, rarity and endemicity are likely among different ecoregions (Emanuel et al. 1992, Roberts et al. 2003a, Ceccherelli et al. 2006, Blanchette et al. 2009, Sink et al. 2010). MPAs can also be designed based on functional groups that are present, to ensure that various groups of species that perform different functions in the ecosystem are protected, and ecosystem functioning can be maintained (Roberts et al. 2003b). Proper planning that helps to minimise threats to biodiversity in a given area is important prior to the selection of an area as an MPA, as it can inform the optimal selection of MPAs and management strategies, and reduce costs necessary for effective protection (Roberts 2000, Roberts et al. 2003a, b, Zupan et al. 2018). To ensure that MPAs reach full potential, high compliance and enforcement of regulations are crucial.

Despite many benefits having been reported, MPAs have been criticised for focusing only on small-scale ecological aspects and for failing to address emerging issues such as climate change, ocean acidification, plastic pollution and alien and invasive species (Agardy 1994, Fenberg et al. 2012, Hilborn 2018). Clearly, MPAs need to be employed in conjunction with

other management procedures (Keller et al. 2009). Hilborn et al. (2004) and Hilborn (2018) argue that MPAs on their own do not reduce harvesting but simply shift it to another place, causing an increase in harvesting there. In addition, existence of MPAs takes away food and harvesting opportunities for adjacent poor communities through closure of fishing grounds (Fenberg et al. 2012). However, they can also provide alternative sources of livelihoods and other benefits (Sink 2016), including improved fishing in adjacent areas (Kerwath et al. 2013) and net economic gains for the region (Oberholzer et al. 2010).

Table Mountain National Park (TMNP) MPA is a protected area fringing the metropolis of Cape Town, and was proclaimed in 2004 under the Marine Living Resources Act, by combining existing small marine reserves that were assessed and found to be in need of more effective integration. TMNP MPA is located on the transition zone between the Southern Benguela Ecoregion and the Agulhas Ecoregion (Tunley 2009, Sink et al. 2019). As a result of its pivotal position at this boundary, the MPA contains a high diversity of marine species. The influence of coastal upwelling makes it highly productive and a prime spot for fishing by surrounding communities. The MPA was rezoned in 2004 into six no-take ('restricted') areas that are interspersed with 'controlled' areas (Fig. 2.1) to allow different levels of access and human activities, with all harvesting and fishing being prohibited in no-take areas and normal fisheries and environmental regulations being enforced in 'controlled' areas.

Overexploitation of fish and invertebrates, poaching, pollution and alien species have been identified as major anthropogenic pressures facing the TMNP MPA (Brill 2012, Brill & Raemaekers 2013). Apart from overexploitation, studies show that illegal fishing – poaching – has increased in TMNP MPA in the past decade (Crookes 2016). Poaching affects various intertidal rocky shore species including limpets (*Cymbula* spp., *Scutellastra* spp.), mussels (*Choromytilus meridionalis*, *Mytilus galloprovincialis*), alikreukel (*Turbo sarmaticus*), abalone (*Haliotis* spp.), octopus (*Octopus vulgaris*) and red bait (*Pyura stolonifera*), as well as shallow-water species like abalone (*Haliotis midae*) and rock lobster (*Jasus lalandii*) (Brill & Raemaekers 2013). The rocky shores are additionally infested with alien invasive species, most notably the Pacific barnacle *Balanus glandula*, the Mediterranean mussel *Mytilus galloprovincialis* and the bisexual mussel *Semimytilus algosus* (Robinson et al. 2005, Laird & Griffiths 2008, Reimers et al. 2014, Pfaff et al. 2019). Thus, there is an urgent need to assess the effectiveness of the MPA in controlling the effects of anthropogenic impacts on the ecological integrity of rocky shore ecosystems.

This dissertation is aimed at evaluating the effectiveness of TMNP MPA in protecting rocky shore communities or, to be more precise, whether no-take areas within the park are more effective in protecting biodiversity than 'controlled' areas where harvesting is permitted. It comprises the present introductory chapter (Chapter 1), followed by three substantive chapters as follows. Chapter 2 compares sizes and densities of key species and community composition in areas that are zoned for harvesting with no-take areas within the TMNP MPA. Because of the physical complexity of the MPA, replicated and matched pairs of sites are compared on the West and East coasts of the Peninsula, and on the two main types of rock (sandstone and granite). Chapter 3 narrows the focus to three harvested and two fully protected sites on the west coast, all situated on Table Mountain Sandstone. These sites were employed for a more detailed analysis because historical data exist for some of them, allowing a more complete temporal and spatial comparison of differences in densities, sizes and community composition over time. In Chapter 4, the effects of removing a key grazer, the limpet *Cymbula granatina*, on community composition, are explored in an experimental manipulation that established different densities of this limpet at two sites within a fully-protected section of the MPA. Finally, I present a brief synopsis of the dissertation and its implications in Chapter 5.

# Chapter 2: Effects of protection, biogeography and rock type on the sizes and densities and of key species and the composition of intertidal rocky-shore communities


## Abstract

This study assesses the effectiveness of Table Mountain National Park MPA in protecting the biodiversity of intertidal rocky shores from impacts of harvesting. Surveys were conducted in harvested and no-take areas to compare the densities and sizes of exploited species and the community composition between intertidal rocky shores experiencing these different levels of protection, in two ecoregions and on two types of rock substrate. Some clear patterns emerged. Firstly, no-take areas had significantly greater densities of the limpets *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei*, particularly on sandstone shores, relative to their abundance in areas where these species are commonly harvested. Conversely, densities of the rarely harvested limpets *S. cochlear*, *S. longicosta* and *S. granularis* did not differ in any manner consistent with protection levels. Secondly, *C. granatina* and *S. argenvillei* were significantly larger in no-take areas, although *C. oculus* displayed the opposite pattern. None of the rarely harvested limpets showed differences in sizes between protection levels. Thirdly, community composition differed significantly between protection levels. No-take areas were characterised by greater abundances of harvested limpets and mussels, while harvested areas were dominated by ephemeral and corticated algae, which flourished under reduced grazing pressure by limpets. My study provided congruent evidence that no-take areas within this MPA are effective in maintaining a natural community composition and densities and size structures of exploited species on rocky shores, providing evidence in support of the management success of no-take areas in the Table Mountain National Park.


## Introduction

Harvesting has been identified as a major threat to rocky shore biodiversity worldwide. Stocks of many species have been depleted and a growing number of species are facing extinction due to overexploitation (Lasiak 1991a, Mannino & Thomas 2001, Espinosa et al. 2006, 2009, 2014, Coppa et al. 2012, 2015). Overharvesting of limpets, for example, may indirectly have contributed to the extinction of the Canarian black oystercatcher *Haematopus meadewaldi*, which relied on limpets as one of its main sources of food (Hockey, 1987). To reduce harvesting pressure and allow for the recovery of overexploited species, Marine Protected Areas (MPAs) have been established (Hockey & Branch 1997, Parnell et al. 2005, Maneveldt et al. 2009, Coppa et al. 2012, 2015, López et al. 2012, Marra et al. 2017). However, critics argue that there are more effective management tools available than MPAs for ensuring protection, and that

they come at a lower cost in terms of food production (Hilborn 2018). To justify to society the maintenance of existing MPAs and proclamation of new MPAs and their associated costs, it is thus essential to assess and evaluate MPA performance and effectiveness in terms of biodiversity protection, as well as human benefits, against set objectives (Ban et al. 2019).

Harvesting has direct and indirect impacts on rocky shore organisms. Humans tend to selectively remove preferred species and larger individuals, driving some species to the point of extinction (Espinosa & Rivera-Ingram 2017, Carballo et al. 2019). This has the potential to alter genetic composition (Fenberg & Roy 2008), and commonly reduces densities, average sizes and ages of target species (Hockey & Bosman 1986, Hockey et al. 1988, Durán & Castilla 1989, Lasiak 1998, Keough et al 1993, Mannino & Thomas 2001, Branch & Odendaal 2003, Fraschetti et al. 2005a, Micheli et al. 2005, Parnell et al. 2005, Rius et al. 2006, Sagarin et al. 2007, Martins et al. 2008, Ramírez et al. 2009, Coppa et al. 2012, López et al. 2012, Zarrouk et al. 2016, Marra et al. 2017). As a result, higher densities and larger sizes of frequently harvested organisms are common inside MPAs compared to outside, as has been reported, for example, for the limpets *Helcion concolor* (Branch 1975a), *Cymbula oculus* (Branch & Odendaal 2003), *Fissurella crassa*, *F. limbata* (Godoy & Moreno 1989, Durán & Castilla 1989), *Lottia gigantea* (Sagarin et al. 2007, Fenberg & Roy 2012), several European species of *Patella* (Parnell et al. 2005, Espinosa et al. 2009, López et al. 2012, Muñoz-Colmenero et al. 2012, Zarrouk et al. 2016, Marra et al. 2017), the mussel *Perna perna* (Lasiak 1998, Rius et al. 2006) and other mussels (Rius & Zabala 2008), and the urchin *Strongylocentrotus franciscanus* (Tuya et al. 2000). Similar responses have been documented for many other intertidal and shallow-water species (Hockey & Bosman 1986, Hockey et al. 1988, Lasiak & Field 1995, García-Charton et al. 2000, Ceccherelli et al. 2006, Martins et al. 2008, Nakin et al. 2012, Deepananda & Macusi 2012, 2013, Fraschetti et al. 2013, Ferreira et al. 2017).

However, in some cases, the establishment of MPAs does not produce such patterns in harvested populations, and can even be associated with a decline in the densities of some species because they experience greater predation or competition inside the MPA due to increases in other species – through indirect effects of protection. For example, a decline in sea urchins in Mediterranean marine reserves has been convincingly linked to increases in predatory fish (Guidetti 2006, Giakoumi et al. 2017). Similarly, McClanahan & Muthiga (1988) and McClanahan & Arthur (2001) showed that increases in fish densities inside Kenyan MPAs was associated with substantial declines in urchins. Götz et al. (2009a, b) showed that

as the predatory sparid *Chrysoblephus laticeps* increased in Goukamma MPA in South Africa, numbers of several competitors dropped, and feather stars and algae decreased due to a combination of increased competition and consumption.

In a different vein, densities of harvested species do not always increase inside MPAs. Nakin & McQuaid (2014) recorded similar densities for *Helcion concolor* and *Scutellastra longicosta* inside and outside Dwesa-Cwebe Nature Reserve on the east coast of South Africa, despite both species being harvested in that region. Similarly, community composition did not differ in different zones of the Tuscan Archipelago National Park (Benedetti-Cecchi et al. 2003a) or in Torre Guaceto MPA in the Mediterranean (Fraschetti et al. 2005a). These findings show that the effects of an MPA can be area-specific and species-specific, or reflect the efficiency of enforcement, thus indicating a need to evaluate MPA effects on a case-by-case basis (Benedetti-Cecchi et al. 2003a, Nakin et al. 2012).

The loss of large individuals from herbivorous populations and declines in their density associated with harvesting often alter community composition as the effects of grazing are diminished (Underwood & Jernakoff 1984, Lasiak & Field 1995, Lasiak 1998, Mannino & Thomas 2001, Benedetti-Cecchi et al. 2003a, Fraschetti et al. 2005a, Sagarin et al. 2007). This is associated with weakened interactions between species in the harvested areas. When MPAs are established, the protection of target species strengthens interactions between them and other species and leads to changes in community composition as prey or competitors are driven to lower levels (Durán & Castilla 1989, Lasiak & Field 1995, Lasiak 1998, Benedetti-Cecchi et al. 2003a, Fraschetti et al. 2005a, Rius et al. 2006, Martins et al. 2008). Consequently, community compositions of harvested and no-take areas often differ, as reflected in a dominance of species such as limpets, abalone and mussels in the absence of harvesting, whereas harvested areas tend to be dominated by algae as a result of the removal of grazers (Hockey & Bosman 1986, Lasiak & Field 1995, Martins et al. 2008). By contrast, because of the depletion of a key predator, *Concholepas concholepas*, exploited rocky shores in Chile have become dominated by the mussel *Perumytilus purpuratus* (Durán & Castilla 1989). Heyns-Veale et al. (2019) showed that fish species targeted by fishers increased in abundance and size inside MPAs, whereas species that are not targeted decreased in abundance. In the light of these direct and indirect effects of protection it is important to evaluate the effectiveness of MPAs in conserving rocky shore community composition as a whole, as well as in preserving the demography and dynamics of individual populations (Henriques et al. 2017).

In this study, I examined the effect of the Table Mountain National Park MPA (TMNP MPA) on densities and sizes of key intertidal populations as well as on overall rocky-shore community composition. I approached this by making comparisons between sites that are protected from harvesting (i.e. restricted/no-take areas) and corresponding areas where harvesting is permitted but controlled in the form of bag limits imposed for individual species (i.e. controlled/harvested areas). My primary goal was thus to determine the effectiveness of no-take areas relative to harvested areas in terms of the conservation of representative biotic communities.

Two other factors were also accounted for as they likely affect population and community composition on rocky shores: biogeography and rock type. For species or groups that occur in multiple biogeographic regions (or ecoregions), striking differences in biomasses and/or sizes have been recorded among regions, with greater values on the west coast of South Africa (the Southern Benguela Ecoregion) than on either the south coast (the Agulhas Ecoregion) or the east coast (the Natal Ecoregion) (Bustamante et al. 1995a, 1995b, Bustamante & Branch 1996a, Sink et al. 2019). These differences have been related to a gradient of primary productivity, which is highest on the west coast and decreases eastward. The TMNP MPA spans the interface between two ecoregions (Fig. 2.1) and the design of this study therefore accounted for the potential differences in the population structure of species that occur in both of the ecoregions within the MPA.

The following hypotheses were tested: (1) Sizes of harvested individuals of the frequently harvested species *Cymbula granatina* and *Scutellastra argenvillei* will reflect selective targeting of large individuals. (2) Densities and average sizes of three frequently harvested species, namely the limpets *C. granatina, C. oculus* and *Scutellastra argenvillei*, will be greater in no-take areas than in harvested areas. (3) For three species that are rarely harvested, i.e., *Scutellastra cochlear, S. longicosta* and *S. granularis,* protection by the MPA will not have an effect, and their densities and sizes will not differ between no-take and harvested areas. (4) Differences will exist in community structure between no-take and harvested areas, with functional groups that are susceptible to harvesting being more abundant in no-take than harvested areas. This study thereby constitutes the first comprehensive intertidal assessment of the effectiveness of this MPA in meeting its objective to protect exploited populations and communities, and thereby contributes to an ecosystem-based approach to resource management.

## Materials and methods

*Study design and sites*

The TMNP MPA occupies a transition between the Agulhas and Southern Benguela Ecoregions, with Cape Point constituting a well-known biogeographic break (Emanuel et al. 1992, Tunley 2009, Sink et al. 2019; Fig. 2.1), and a site of reduced gene flow (von der Heyden 2009, Wright et al. 2015). The shores I surveyed lay on both the East and West sides of the Cape Peninsula, thus falling into these two respective ecoregions (Emanuel at al. 1992). The area features diverse rock types, but predominantly comprises Cape Granite and Table Mountain Sandstone (TMS) (McQuaid & Branch 1985, Pfaff et al. 2019). The design of the MPA took this into account, and both of these rock types are represented in no-take (restricted) and harvested (controlled) areas where harvesting is permitted but regulated (Fig. 2.1).

To study the effect of MPA protection level, ecoregion and rock type on rocky shore populations and community structure, 16 sites were selected within the TMNP MPA that represented two protection levels, two ecoregions and two rock types, with two replicate sites of each combination (Table 2.1). Efforts were made to spatially randomise the site selection by placing replicate sites in different no-take areas wherever possible. Wave action was standardised by selecting sites that fell in the range defined as ‘semi-exposed’ to ‘exposed’ by Steffani & Branch (2003), thus avoiding shores classed as ‘sheltered’ or ‘extremely exposed’.

No data existed to quantify the amounts of resources extracted from the sites I studied, so I ranked sites according to relative harvesting levels (Table 2.1) based on (a) accessibility of sites, (b) numbers of people visiting sites (van Herwerden et al. 1989, van Herwerden & Griffiths 1991); (c) daily offence logbooks maintained by South African National Parks (SANParks) rangers; (d) analyses of confiscations and incidences by Brill (2012); (e) historical records (GM Branch unpublished data) of the composition and size-frequencies of intertidal molluscs harvested illegally (reported in the Results), and (f) local knowledge acquired during surveys, coupled with expert inputs from five anonymous conservation authorities. I did not use this ranking in a quantitative manner, but draw on it in the Discussion to better explain patterns that emerged.

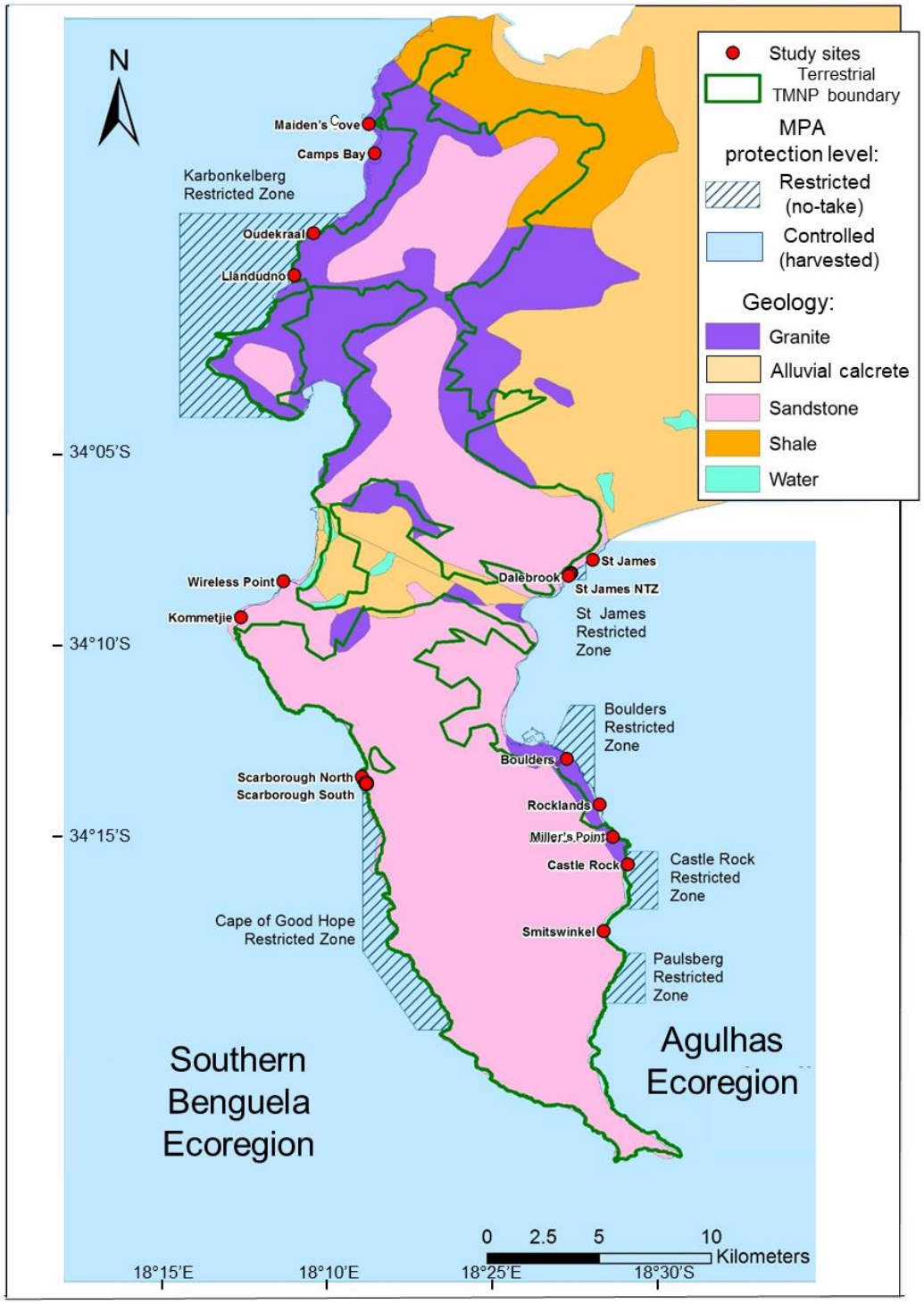



Figure 2.1. Map of the Cape Peninsula showing the Table Mountain National Park Marine Protected Area (TMNP MPA), with Controlled zones where harvesting is permitted (unmarked areas) and Restricted 'no-take' zones (hatched areas). Study sites are marked with red dots, and colour coding indicates different geological formations.

**Table 2.1**. List of study sites with their protection levels, rock type, ecoregion and GPS coordinates, ranked by harvesting levels from 1 (least) to 16 (most). TM Sandstone = Table Mountain Sandstone. Sn Benguela = Southern Benguela; S = South, N = North. For some analyses an additional site, Wireless Island (with the same properties as Wireless Point) was sampled, and lies 40 m offshore of Wireless Point.

| Site | Protection level | Rock Type | Ecoregion | GPS Coordinates | Harvesting level |
|---|---|---|---|---|---|
| St James | Harvested | TM Sandstone | Agulhas | 34°07'23.93"S; 18°27'12.78"E | 14 |
| Smitswinkel | Harvested | TM Sandstone | Agulhas | 34°16'00.67"S; 18°27'59.92"E | 13 |
| St James NTZ | No-take | TM Sandstone | Agulhas | 34°07'25.57"S; 18°27'11.87"E | 7 |
| Dalebrook | No-take | TM Sandstone | Agulhas | 34°07'28.06"S; 18°27'09.21"E | 6 |
| Rocklands | Harvested | Cape Granite | Agulhas | 34°12'58.30"S; 18°27'53.65"E | 8 |
| Millers Point | Harvested | Cape Granite | Agulhas | 34°13'44.76"S; 18°28'13.17"E | 10 |
| Boulders | No-take | Cape Granite | Agulhas | 34°11'52.48"S; 18°27'06.60"E | 5 |
| Castle Rock | No-take | Cape Granite | Agulhas | 34°14'24.36"S; 18°28'34.87"E | 9 |
| Kommetjie | Harvested | TM Sandstone | Sn Benguela | 34°08'27.57"S; 18°19'16.16"E | 16 |
| Wireless Point | Harvested | TM Sandstone | Sn Benguela | 34°07'35.97"S; 18°20'17.32"E | 15 |
| Scarborough S | No-take | TM Sandstone | Sn Benguela | 34°12'21.56"S; 18°22'12.47"E | 1 |
| Scarborough N | No-take | TM Sandstone | Sn Benguela | 34°12'17.89"S; 18°22'10.52"E | 3 |
| Camps Bay | Harvested | Cape Granite | Sn Benguela | 33°57'18.50"S; 18°22'28.98"E | 11 |
| Maiden's Cove | Harvested | Cape Granite | Sn Benguela | 33°56'36.03"S; 18°22'20.23"E | 11 |
| Llandudno | No-take | Cape Granite | Sn Benguela | 34°00'14.01"S; 18°20'33.08"E | 4 |
| Oudekraal | No-take | Cape Granite | Sn Benguela | 33°59'13.45"S; 18°21'00.55"E | 2 |

*Sampling procedure*

Surveys were conducted at all 16 sites. For each site, four intertidal zones were identified based on their relative level and biotic indicators, at heights of approximately +0.2, +0.8, +1.2 and +1.5 m above low water spring tide respectively (mean spring tidal range being 1.87 m). The low shore was usually dominated by *Scutellastra cochlear* and encrusting algae, often together with *S. argenvillei*. The mid shore predominantly featured the algae *Gelidium pristoides* and *Pachymenia orbitosa*, the limpet *Cymbula granatina* and the mussel *Mytilus galloprovincialis*, depending on the biogeographic region. The high shore was characterised by the limpet *Scutellastra granularis*, *M. galloprovincialis* and barnacles, and the top shore by barnacles, the alga *Porphyra* '*capensis*' and *S. granularis*. In each zone, 15 replicate 50x50-cm quadrats (divided into 25 cells of 4% cover each) were randomly placed and visually sampled. In each quadrat, all macro-organisms were identified and quantified as percentage cover for sessile organisms and as counts for mobile fauna (see Bustamante & Branch 1996a, Blamey & Branch 2009). To standardise, counts were later converted to percentage cover (Wieters et al 2009).

Densities and sizes of three limpet species commonly harvested in the region, *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei* (Eekhout et al. 1992, Bustamante et al. 1995a, Branch & Odendaal 2003) were compared with those of three species of limpet rarely harvested there, *S. cochlear*, *S. granularis* (Nakin & McQuaid 2014) and *S. longicosta*. Classification of species as 'commonly harvested or 'rarely harvested' were based on my own observations, as reported in the Results, and those of Lasiak (1991b) and Nakin & McQuaid (2014). These authors do report *Scutellastra longicosta* as being harvested on the south-east coast of South Africa, but I have no evidence of this taking place where I worked. Measurements were made separately in all four intertidal zones within 15 replicate quadrats, with a minimum of 50 individuals being measured per species.

Data for the sizes and relative abundances of shellfish that had been harvested were obtained from SANParks field rangers' records, and opportunistically from confiscated material and discarded shucked shells. These data allowed qualitative commentary on which species are most often harvested, and whether harvesters are selectively collecting larger individuals.

*Data analyses*

To meaningfully compare community composition between the two ecoregions, species were grouped into functional groups (Table 2.2), as the two ecoregions support different species, but comparable functional groups. Grouping may obscure the effects for rare species, but reduces statistical challenges associated with numerous dependent variables (Warton et al. 2012, 2015). Algal grouping was based on morphology related to productivity and susceptibility to herbivory (Steneck & Dethier 1994). Invertebrates were grouped by trophic position and foraging strategy (Wieters et al 2009). Herbivores were divided into 'grazers' cropping algae, 'trappers' snaring drift algae or fronds, and 'gardeners' cultivating patches of algae.

Each zone represents a unique biotope, so intertidal zones were analysed separately. Three-way full-factorial PERMANOVAs of percentage cover tested whether community composition was affected by protection level (no-take vs. harvested), ecoregion (Agulhas vs. Sn Benguela) and rock type (granite vs. sandstone), or their interactions. Data were standardised and square-root transformed to upweight the contribution of rare taxa. The nature of significant differences was explored using Tukey HSD post-hoc tests. Multidimensional scaling (MDS) was employed to visually portray differences in community structure between protection levels, ecoregions and rock types. SIMPER identified functional groups responsible for any observed differences.

To evaluate differences in densities and sizes of selected species between no-take and harvested areas and between granite and sandstone shores, two-way fully-crossed ANOVAs with factors 'protection level' and 'rock type' were applied, after confirming the assumptions of normality and homogeneity of variances using the Shapiro–Wilk and Levene's tests respectively. The absence of *Scutellastra longicosta* at two granite rocky shores led to two-way nested ANOVA, with 'rock type' nested in 'protection level', being performed on the sizes of this species. For four species, the effect of ecoregion was not considered, because they occurred predominantly in only one ecoregion. As *S. cochlear* and *S. granularis* occur in both ecoregions, ecoregion was added as a variable, and three-factorial ANOVAs employed. Where significant differences or interactions were found, post-hoc Tukey tests were used to explore their nature. Student's t-tests were used to compare the mean sizes of *Cymbula granatina* individuals collected by harvesters at Wireless Point and Kommetjie and those present on the shore at these respective sites and, likewise, for *Scutellastra argenvillei* at Wireless Island. All statistical analyses were performed with the R package (R Core Team 2019), using car package (Fox & Weisberg 2019).

**Table 2.2**. The functional groups assignment of species of algae and invertebrates used in this study, modified from Wieters et al. (2009).

| **Ephemeral algae** | **Corticated algae** | **Articulated algae** | **Filter Feeders** | **Grazers** | **Other herbivores** | **Predators & Scavengers** |
|---|---|---|---|---|---|---|
| *Callithamnion collabens* | *Ahnfeltiopsis polyclada* | *Arthrocardia* spp. | *Aulacomya atra* | *Afrolittorina knysnaensis* | | *Argobuccinum pustulosum* |
| *Caulacanthus* spp. | *Bifurcariopsis capensis* | *Cheilosporum* spp. | *Balanus glandula* | *Acanthochitona garnoti* | **Gardeners** | *Burnupena catarrhacta* |
| *Centroceras* spp. | *Brassicophycus brassicaeformis* | *Corallina* spp. | *Chthamalus dentatus* | *Chiton polita* | *Scutellastra cochlear* | *Burnupena cincta* |
| *Ceramium* spp. | *Champia lumbricalis* | *Jania* spp. | *Crepidula porcellana* | *Cymbula miniata* | *Scutellastra longicosta* | *Burnupena lagenaria* |
| *Chaetomorpha* spp. | *Chordariopsis capensis* | | *Dendropoma corallinaceus* | *Cymbula granatina* | | *Burnupena papyracea* |
| *Cladophora* spp. | *Chylocladia capensis* | **Algal crusts** | *Dodecaceria pulchra* | *Cymbula oculus* | **Trappers** | *Parvulastra exigua* |
| *Polysiphonia* spp. | *Codium fragile* | | *Hymeniacidon perlevis* | *Fissurella* spp. | | *Trochia* (*Nucella*) *cingulata* |
| *Porphyra* spp. | *Gelidium micropterum* | *Black crust* | *Gunnarea gaimardi* | *Haliotis spadicea* | ‡ *Cymbula granatina* | |
| *Ulva* spp. | *Gelidium pristoides* | *Hildenbrandia* spp. | *Mytilus galloprovincialis* | *Helcion dunkeri* | † *Scutellastra argenvillei* | **Anemones** |
| | *Gelidium reptans* | *Ralfsia verrucosa* | *Notomegabalanus algicola* | *Helcion pectunculus* | | |
| **Kelp** | *Gigartina polycarpa* | *Chamberlainium* spp. | *Octomeris angulosus* | *Oxystele antoni* | | *Actinia ebhaiensis* |
| | *Grateloupia capensis* | | *Pyura stolonifera* | *Oxystele tigrina* | | *Anthothoe stimpsonii* |
| *Ecklonia maxima* | *Gymnogongrus dilatatus* | | *Tetraclita serrata* | *Oxystele sinensis* | | *Anthopleura michaelseni* |
| *Laminaria pallida* | *Hypnea spicifera* | | *Semimytilus algosus* | *Oxystele impervia* | | *Bunodosoma capense* |
| | *Iyengaria stellata* | | *Roweia stephensoni* | *Parechinus angulosus* | | *Bunodactis reynaudi* |
| | *Laurencia flexousa* | | | *Scutellastra barbara* | | |
| | *Leathesia marina /Colpomenia sinuosa* | | | *Scutellastra granularis* | | |
| | *Mazzaella capensis* | | | *Siphonaria capensis* | | |
| | *Nothogenia ovalis* | | | *Siphonaria concinna* | | |
| | *Pachymenia orbitosa* | | | *Siphonaria* spp. | | |
| | *Plocamium cornutum* | | | *Turbo sarmaticus* | | |
| | *Plocamiun corallorhiza* | | | | | |
| | *Plocamiun rigidum* | | | | | |
| | *Pterosiphonia cloiophylla* | | | | | |
| | *Sarcothalia stiriata* | | | | | |
| | *Splachnidium rugosum* | | | | | |

‡ individuals > 30 mm regarded as 'trappers' of drift algae
† individuals > 40 mm regarded as 'trappers' of drift algae

## Results

### *Abundances and sizes of limpets collected by harvesters*

Harvesters at Kommetjie, Wireless Point and Wireless Island targeted three species of limpets, together with the mussels *Choromytilus meridionalis* and *Mytilus galloprovincialis* (Table 2.3). The limpet *C. granatina* was the most harvested taxon while other species featured less often in collections, and *Scutellastra barbara* scarcely at all. *Scutellastra argenvillei* was recorded as being collected only at Wireless Island. Two limpet species, *S. cochlear* and *S. granularis* were never taken.

Harvesters focused on large individuals of *C. granatina* and *S. argenvillei* (Fig. 2.2), with the smallest harvested individual being respectively 40-45 mm and 60 mm, whereas natural populations had individuals as small as 5-20 mm. Differences in mean sizes between harvested and natural populations were significant at all three sites ($p \leq 0.002$; Fig. 2.2).

**Table 2.3.** Number of individuals harvested for seven species of commonly and rarely harvested species in Kom = Kommetjie, WI = Wireless Island and WP = Wireless Point.

| Date | Site | *C. granatina* | *C. oculus* | *S. barbara* | *S. argenvillei* | Mussels | *S. cochlear* | *S. granularis* |
|---|---|---|---|---|---|---|---|---|
| 23/10/1985 | WI | 42 | 5 | 0 | 40 | | 0 | 0 |
| 23/10/1985 | WP | 42 | 11 | 1 | | 12 | 0 | 0 |
| 14/8/2005 | WP | 300 | 40 | 4 | | | 0 | 0 |
| 21/12/2014 | WP | 19 | 3 | 1 | | 125 | 0 | 0 |
| 23/11/2014 | WP | 19 | 3 | 1 | | 45 | 0 | 0 |
| 25/04/2017 | Kom | 280 | 47 | 0 | | | 0 | 0 |
| TOTALS | | 702 | 109 | 7 | 40 | 182 | 0 | 0 |

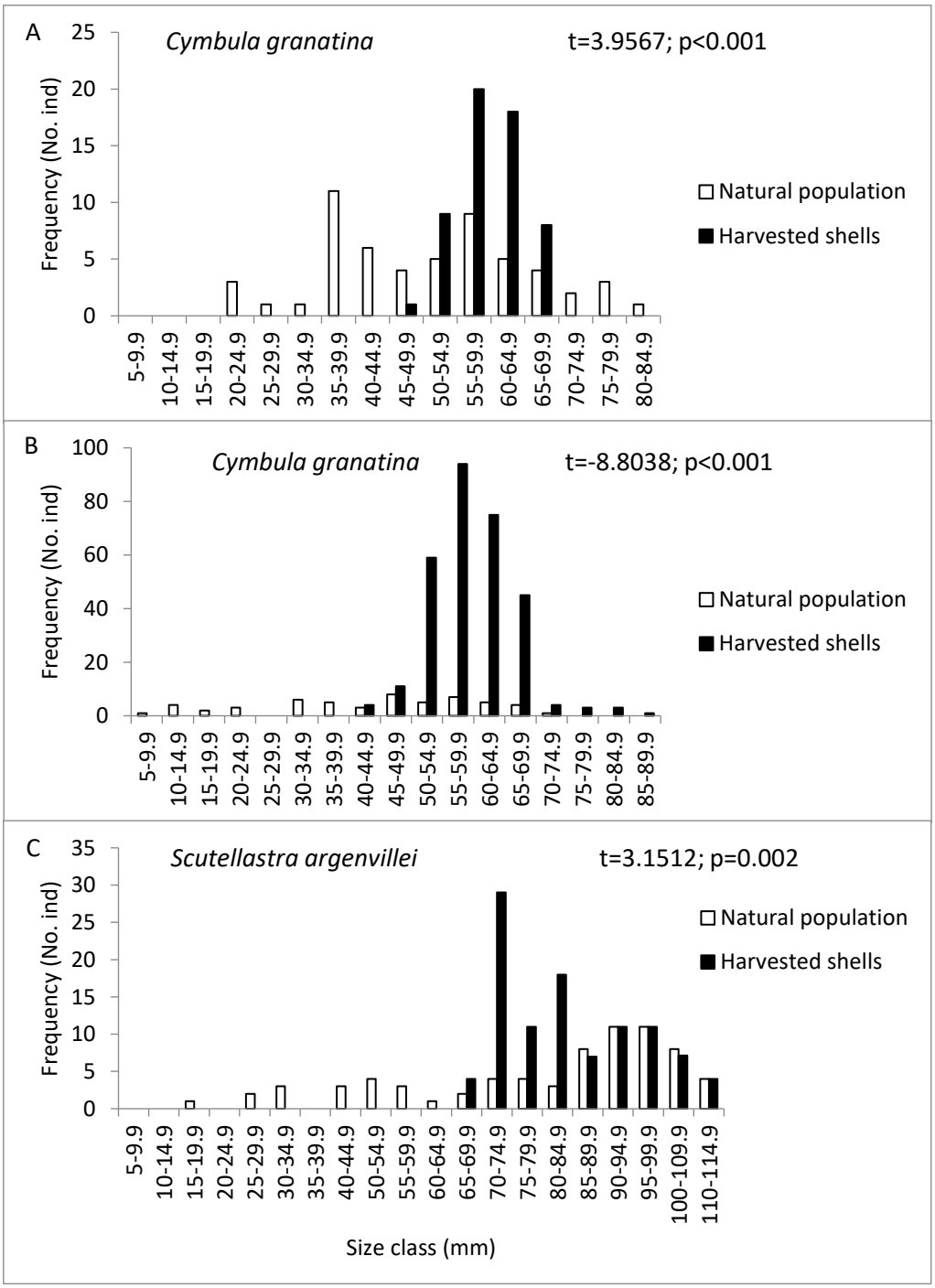



Figure 2.2. Comparisons of shell lengths of harvested individuals and those in natural populations, for (A) *C. granatina* at Kommetjie (B) *C. granatina* at Wireless Point and (C) *S. argenvillei* at Wireless Island. T-test values and probabilities are shown for each species.

*Densities of key species*

There were significant interactions between rock type and protection effects on densities for all three commonly harvested limpet species, *Cymbula granatina*, *C. oculus* and *Scutellastra argenvillei* (Table 2.4), so that post-hoc comparisons were necessary to interpret the effects of protection. On sandstone shores, there were significantly greater densities of all three commonly harvested limpets in the no-take areas compared to harvested sites, while on granite shores, where average densities were lower, no differences existed between no-take and harvested sites (Fig. 2.3A-C).

In contrast, the rarely harvested *S. longicosta* did not differ in abundance between levels of protection (Table 2.4, Fig. 2.3D), and was the only species examined that exhibited a consistent pattern with respect to rock type, being more abundant on sandstone than granite.

For the second rarely harvested limpet, *S. cochlear*, protection had no significant main effect on densities (Table 2.5). Significant interactions among all factors arose because greater densities occurred inside no-take areas on Southern Benguela sandstone, while granite rocks in the same ecoregion had significantly fewer *S. cochlear* in no-take areas. In the Agulhas Ecoregion, *S. cochlear* exhibited no differences between no-take and harvested areas (Fig. 2.3E). In short, there was no consistent effect of protection for this species.

The third rarely harvested limpet, *Scutellastra granularis*, attained equivalent densities between harvested and no-take areas in the Agulhas Ecoregion, whereas lower densities were found on harvested rocks than in no-take areas for granite rocky shores in the Southern Benguela Ecoregion (Table 2.5; Fig. 2.3F).

**Table 2.4**. Results of two-way ANOVAs to assess the effects of protection level and rock type on the densities of species that occurred only in one ecoregion: *Cymbula granatina*, *C. oculus*, *S. argenvillei* (frequently harvested) and *S. longicosta* (rarely harvested). Asterisks indicate significant effects.

| Source | df | SS | MS | F | P-value |
|---|---|---|---|---|---|
| *C. granatina* | | | | | |
| Protection | 1 | 1239 | 1239 | 23.37 | <0.001* |
| Rock type | 1 | 3002 | 3002 | 56.60 | <0.001* |
| Protection x Rock | 1 | 1359 | 1359 | 25.63 | <0.001* |
| Residuals | 354 | 18772 | 53 | | |
| *C. oculus* | | | | | |
| Protection | 1 | 3.4 | 3.405 | 3.069 | 0.081 |
| Rock type | 1 | 24.6 | 24.587 | 22.156 | <0.001* |
| Protection x Rock | 1 | 31.2 | 31.216 | 28.129 | <0.001* |
| Residuals | 355 | 394.0 | 1.110 | | |
| *S. argenvillei* | | | | | |
| Protection | 1 | 891 | 891.1 | 11.874 | 0.001* |
| Rock type | 1 | 357 | 357.1 | 4.758 | 0.031* |
| Protection x Rock | 1 | 1038 | 1038.4 | 13.838 | <0.001* |
| Residuals | 116 | 8705 | 75.0 | | |
| *S. longicosta* | | | | | |
| Protection | 1 | 1.97 | 1.970 | 3.512 | 0.062 |
| Rock type | 1 | 12.39 | 12.395 | 22.094 | <0.001* |
| Protection x Rock | 1 | 1.87 | 1.867 | 3.328 | 0.069 |
| Residuals | 232 | 130.15 | 0.561 | | |

**Table 2.5**. Results of three-way ANOVAs to assess the effect of protection level (Prot), ecoregion (Eco) and rock type (Ro) on the densities of the two rarely harvested limpet species that occurred in both Southern Benguela and Agulhas ecoregions. Asterisks indicate significant effects.

| Source | Df | SS | MS | F-value | P-value |
|---|---|---|---|---|---|
| *S. cochlear* | | | | | |
| Ecoregion | 1 | 26072 | 26072 | 9.784 | 0.002* |
| Protection | 1 | 6465 | 6465 | 2.426 | 0.121 |
| Rock type | 1 | 338549 | 338549 | 127.042 | <0.001* |
| Prot x Eco | 1 | 208 | 208 | 0.078 | 0.780 |
| Eco x Ro | 1 | 61249 | 61249 | 22.984 | <0.001* |
| Prot x Ro | 1 | 99485 | 99485 | 37.332 | <0.001* |
| Prot x Eco x Ro | 1 | 63959 | 63959 | 24.001 | <0.001* |
| Residuals | 229 | 610255 | 2665 | | |
| *S. granularis* | | | | | |
| Ecoregion | 1 | 895 | 895 | 4.927 | 0.027* |
| Protection | 1 | 1874 | 1874 | 10.317 | 0.001* |
| Rock type | 1 | 6404 | 6404 | 35.262 | <0.001* |
| Prot x Eco | 1 | 2464 | 2464 | 13.567 | 0.002* |
| Eco x Ro | 1 | 50 | 50 | 0.275 | 0.600 |
| Prot x Ro | 1 | 4428 | 4428 | 24.383 | <0.001* |
| Prot x Eco x Ro | 1 | 16 | 16 | 0.090 | 0.764 |
| Residuals | 945 | 171628 | 182 | | |

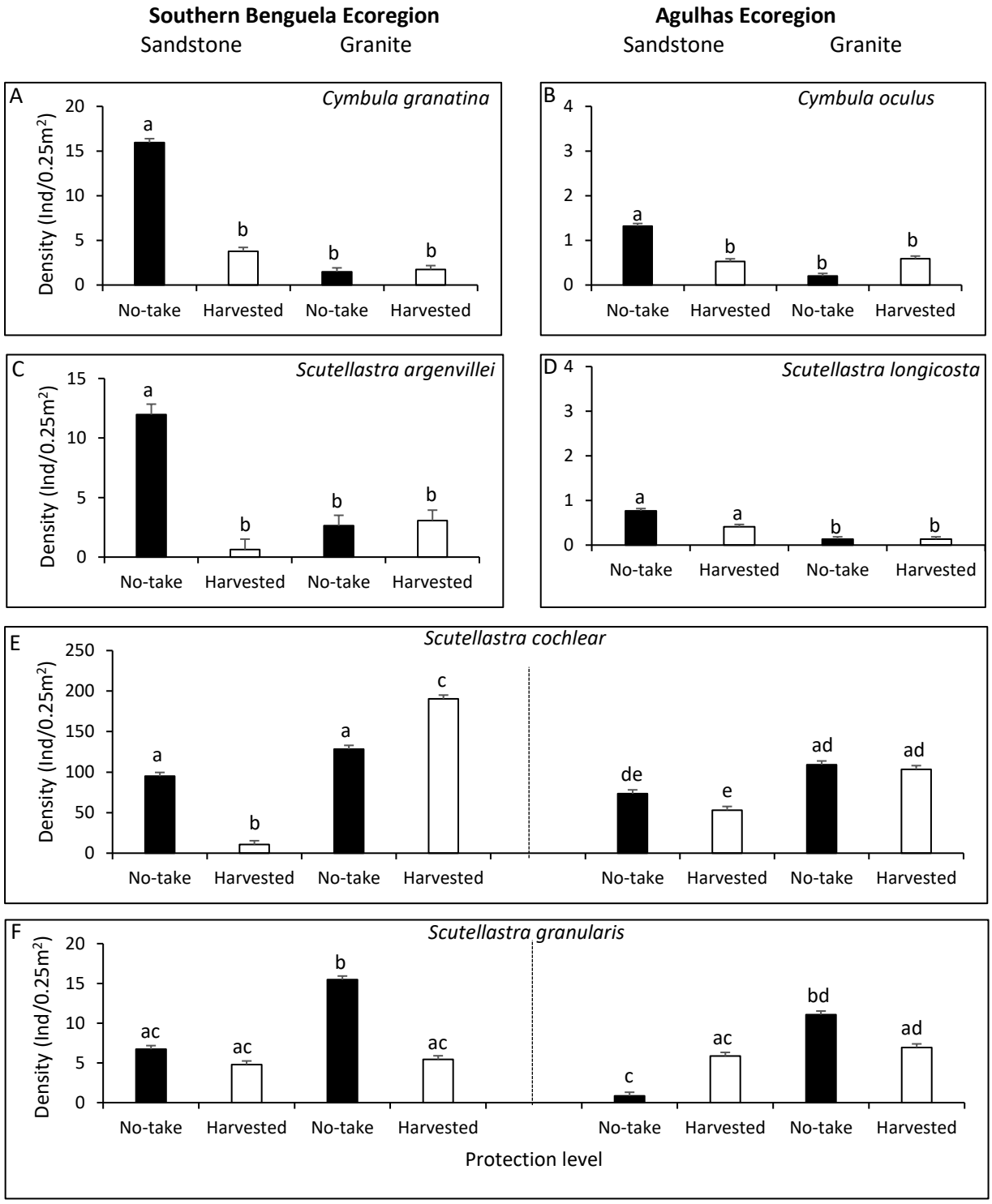



Figure 2.3. Differences in mean densities (+1SE) of frequently harvested (A-C) and rarely harvested (D-F) limpets with regard to protection level and rock type. The first four species (A-D) occur predominantly in only one ecoregion, so this factor was not included for their analysis, but was included in the analysis for fifth and sixth species, *S. cochlear* (E) and *S. granularis* (F) which occur in both ecoregions. Note differences in scale among panels. Ind = number of individuals. Different letters on top of the error bars indicate significant differences.

*Sizes of key species*

Of the commonly harvested limpets, *Cymbula granatina* was significantly larger inside the no-take than the harvested areas but unaffected by rock type (Table 2.6; Fig. 2.4A). *Cymbula oculus* was counterintuitively larger in the harvested areas, but only significantly so for sandstone shores. Again, rock type had no effect on size (Table 2.6; Fig. 2.4B). *Scutellastra argenvillei* was larger in the no-take than harvested areas, but on sandstone shores only, with protection having no effect on granite rocks, hence the significant interaction between protection and rock type (Table 2.6; Fig. 2.4C).

For the first of the limpet species that are rarely or never harvested, *S. longicosta*, size was not affected by either protection level or rock type (Table 2.6; Fig. 2.4D). The sizes of the second rarely harvested limpet, *S. cochlear*, were greater in harvested than no-take areas in the Agulhas ecoregion on granite, but nowhere else (Table 2.7; Fig. 2.4E), with consequent significant interactions. Ecoregional differences also existed for *S. cochlear*, which was consistently larger in the Agulhas than the Southern Benguela Ecoregion (Table 2.6, Fig. 2.4E). For the third rarely harvested limpet, *S. granularis*, sizes were also consistently larger in harvested areas, but significantly so in only two of the four cases (Table 2.7; Fig. 2.4F). Its sizes were also greater in the Southern Benguela than Agulhas, but only in two of four cases, with consequent interactions among protection level, ecoregion and rock type. Three-way interactions existed for *S. granularis* because of the inconsistencies in the effects of protection among regions and rock types.

**Table 2.6**. Two-way ANOVA on the effect of protection level (Prot) and rock type (Ro) (as well as their interaction) on the sizes of the four limpet species that occurred predominantly in a single ecoregion. A two-way nested ANOVA was used for *S. longicosta* due to its absence at two granite sites; hence no interaction is shown. Asterisks indicate significant effects.

| Source | Df | SS | MS | F-value | P-value |
|---|---|---|---|---|---|
| *C. granatina* | | | | | |
| Protection | 1 | 64.7 | 64.74 | 32.813 | <0.001* |
| Rock type | 1 | 1.4 | 1.41 | 0.714 | 0.399 |
| Prot x Ro | 1 | 0.1 | 0.08 | 0.042 | 0.838 |
| Residuals | 310 | 611.6 | 1.97 | | |
| *C. oculus* | | | | | |
| Protection | 1 | 3923 | 3923 | 20.427 | <0.001* |
| Rock type | 1 | 308 | 308 | 1.602 | 0.206 |
| Prot x Ro | 1 | 364 | 364 | 1.893 | 0.169 |
| Residuals | 485 | 93136 | 192 | | |
| *S. argenvillei* | | | | | |
| Protection | 1 | 83.2 | 83.20 | 49.155 | <0.001* |
| Rock type | 1 | 9.8 | 9.80 | 5.800 | 0.016* |
| Prot x Ro | 1 | 11.4 | 11.39 | 6.726 | 0.010* |
| Residuals | 368 | 622.9 | 1.69 | | |
| *S. longicosta* | | | | | |
| Protection | 1 | 2.69 | 2.68 | 2.686 | 0.136 |
| Ro (Prot) | 1 | 44 | 44.40 | 0.218 | 0.641 |
| Residuals | 249 | 298 | 1.19 | | |

**Table 2.7** Results of the three-way ANOVA on the effect of protection level (Prot), ecoregion (Eco) and rock type (Ro) on shell lengths of *S. cochlear* and *S. granularis*. Asterisks indicate significant effects.

| Source | df | SS | MS | F-value | P-value |
|---|---|---|---|---|---|
| *S. cochlear* | | | | | |
| Ecoregion | 1 | 247.2 | 247.24 | 173.959 | <0.001* |
| Protection | 1 | 14.0 | 13.96 | 9.821 | 0.001* |
| Rock type | 1 | 1.1 | 1.13 | 0.793 | 0.373 |
| Eco x Prot | 1 | 1.2 | 1.18 | 0.829 | 0.363 |
| Eco x Ro | 1 | 34.6 | 34.57 | 24.327 | <0.001* |
| Prot x Ro | 1 | 21.4 | 21.37 | 15.040 | <0.001* |
| Eco x Prot x Ro | 1 | 1.0 | 1.05 | 0.738 | 0.391 |
| Residuals | 840 | 1194.2 | 1.42 | | |
| *S. granularis* | | | | | |
| Ecoregion | 1 | 26.1 | 26.11 | 26.301 | <0.001* |
| Protection | 1 | 63.3 | 63.27 | 63.731 | <0.001* |
| Rock type | 1 | 4.7 | 4.73 | 4.766 | 0.029* |
| Eco x Prot | 1 | 5.6 | 5.58 | 5.618 | 0.018* |
| Bio x Ro | 1 | 5.7 | 5.70 | 5.739 | 0.017* |
| Prot x Ro | 1 | 6.9 | 6.94 | 6.993 | 0.008* |
| Eco x Prot x Ro | 1 | 19.8 | 19.80 | 19.940 | <0.001* |
| Residuals | 1204 | 1195.4 | 0.99 | | |

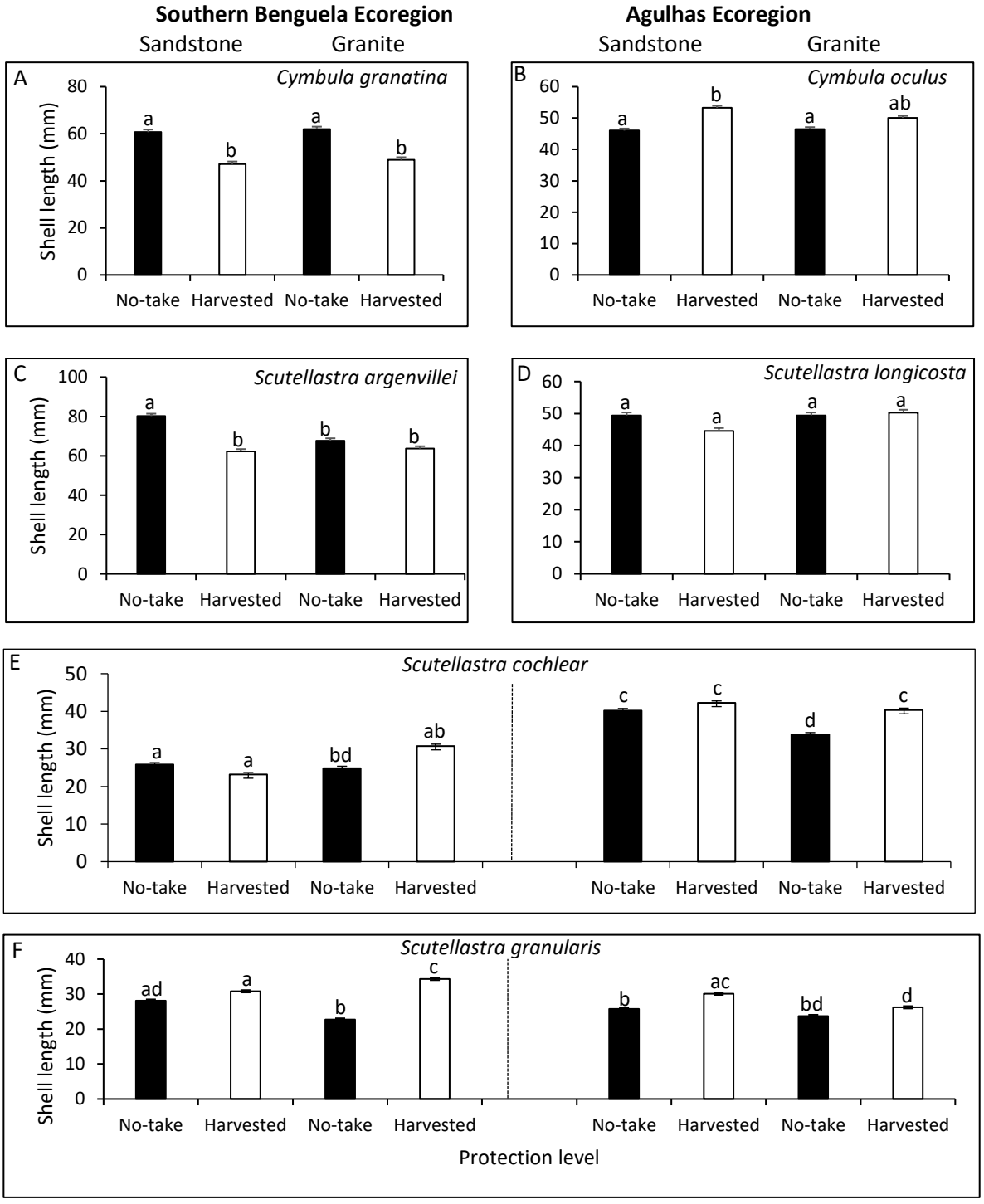



Figure 2.4. Mean shell lengths (+SE) of the commonly harvested limpets (A) *C. granatina*, (B) *C. oculus* and (C) *S. argenvillei*, and the rarely harvested limpets (D) *S. longicosta*, (E) *S. cochlear* and (F) *S. granularis*, in relation to protection levels, rock types and ecoregions (in the case of species that occurred in both ecoregions). Different letters on top of the error bars indicate significant differences.

*Community composition*

In terms of functional-group community composition, there were significant 2-way and 3-way interactions among the factors protection, ecoregion and rock type (Table 2.8), reflecting the fact that the effects of protection on community composition differed between ecoregions and rock types. The high shore stood out as being the only zone in which there was no main effect of protection. In 13 out of 16 pairwise (post-hoc) comparisons of the two states of protection, significant differences in community composition were evident between no-take and harvested areas in both ecoregions, and on both sandstone and granite shores (Table 2.9).

MDS plots exhibited a clear biogeographic distinction between the Southern Benguela and Agulhas ecoregions in all four zones, despite the analysis being based on functional groups and not species (Fig. 2.5). For the Southern Benguela Ecoregion, protection led to marked differences in community composition between harvested and no-take areas in all zones of both rock types, except for mid shore granite (Table 2.9). The MDS plots reflected this, with separate clusters for harvested and no-take sites emerging in all cases except mid shore granite (Fig. 2.5).

For the Agulhas Ecoregion, protection yielded significant effects on the community composition of all sandstone shores except in the top zone (Table 2.9). Again, on granite shores, mid-shore community composition did not differ significantly between harvested and no-take areas, but differences did exist in the other zones (Table 2.9). MDS plots reflected these outcomes, clustering together harvested areas and no-take areas of the top shore zone on sandstone and of the mid shore of granite rocks, while forming discrete clusters in the remaining comparisons (Fig. 2.5).

**Table 2.8**. PERMANOVA of rocky-shore community composition in four different intertidal zones in the TMNP-MPA testing for the effects of protection level (Prot), ecoregion (Eco) and rock type (Ro), and their interactions. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| **Low shore** | | | | | |
| Protection | 1 | 8793.4 | 8793.4 | 17.763 | 0.001* |
| Ecoregion | 1 | 33290 | 33290 | 67.246 | 0.001* |
| Rock type | 1 | 5692 | 5692 | 11.498 | 0.001* |
| Prot x Eco | 1 | 3622 | 3622 | 7.3165 | 0.001* |
| Prot x Ro | 1 | 8245.3 | 8245.3 | 16.655 | 0.001* |
| Eco x Ro | 1 | 3632.4 | 3632.4 | 7.3374 | 0.001* |
| Prot x Eco x Ro | 1 | 4289.1 | 4289.1 | 8.6639 | 0.001* |
| **Mid shore** | | | | | |
| Protection | 1 | 8120.3 | 8120.3 | 9.2875 | 0.001* |
| Ecoregion | 1 | 36262 | 36262 | 41.475 | 0.001* |
| Rock type | 1 | 45191 | 45191 | 51.687 | 0.001* |
| Prot x Eco | 1 | 7566 | 7566 | 8.6535 | 0.001* |
| Prot x Ro | 1 | 8097.2 | 8097.2 | 9.2611 | 0.001* |
| Eco x Ro | 1 | 29071 | 29071 | 33.25 | 0.001* |
| Prot x Eco x Ro | 1 | 3640.6 | 3640.6 | 4.1639 | 0.004* |
| **High shore** | | | | | |
| Protection | 1 | 851.45 | 851.45 | 0.85209 | 0.522 |
| Ecoregion | 1 | 56153 | 56153 | 56.196 | 0.001* |
| Rock type | 1 | 32292 | 32292 | 32.317 | 0.001* |
| Prot x Eco | 1 | 4680.2 | 4680.2 | 4.6837 | 0.001* |
| Prot x Ro | 1 | 9259.1 | 9259.1 | 9.2661 | 0.001* |
| Eco x Ro | 1 | 19437 | 19437 | 19.452 | 0.001* |
| Prot x Eco x Ro | 1 | 15366 | 15366 | 15.378 | 0.001* |
| **Top shore** | | | | | |
| Protection | 1 | 3539.8 | 3539.8 | 4.545 | 0.011* |
| Ecoregion | 1 | 25984 | 25984 | 33.363 | 0.001* |
| Rock type | 1 | 10026 | 5012.8 | 6.4364 | 0.001* |
| Prot x Eco | 1 | 9601.7 | 9601.7 | 12.328 | 0.001* |
| Prot x Ro | 1 | 15664 | 7831.8 | 10.056 | 0.001* |
| Eco x Ro | 1 | 2046.9 | 2046.9 | 2.6282 | 0.061 |
| Prot x Eco x Ro | 1 | 10593 | 10593 | 13.601 | 0.001* |

**Table 2.9**. The pairwise comparisons (posthoc tests) of community compositions between harvested areas and no-take areas for different rock types (Sandstone and Cape Granite) and ecoregion (Southern Benguela and Agulhas). Asterisks indicate significant effects.

| Ecoregion | Rock type | Zone | t-value (Harvested vs. No-take) | P |
|---|---|---|---|---|
| **Southern Benguela** | **Sandstone** | | | |
| | | Low shore | 4.534 | 0.001* |
| | | Mid shore | 6.016 | 0.001* |
| | | High shore | 3.704 | 0.001* |
| | | Top shore | 3.145 | 0.001* |
| | **Cape Granite** | | | |
| | | Low shore | 1.999 | 0.017* |
| | | Mid shore | 1.387 | 0.144 |
| | | High shore | 2.311 | 0.001* |
| | | Top shore | 4.564 | 0.001* |
| **Agulhas** | **Sandstone** | | | |
| | | Low shore | 2.923 | 0.001* |
| | | Mid shore | 2.659 | 0.001* |
| | | High shore | 2.220 | 0.012* |
| | | Top shore | 1.391 | 0.135 |
| | **Cape Granite** | | | |
| | | Low shore | 2.643 | 0.001* |
| | | Mid shore | 1.351 | 0.130 |
| | | High shore | 3.250 | 0.001* |
| | | Top shore | 3.488 | 0.001* |

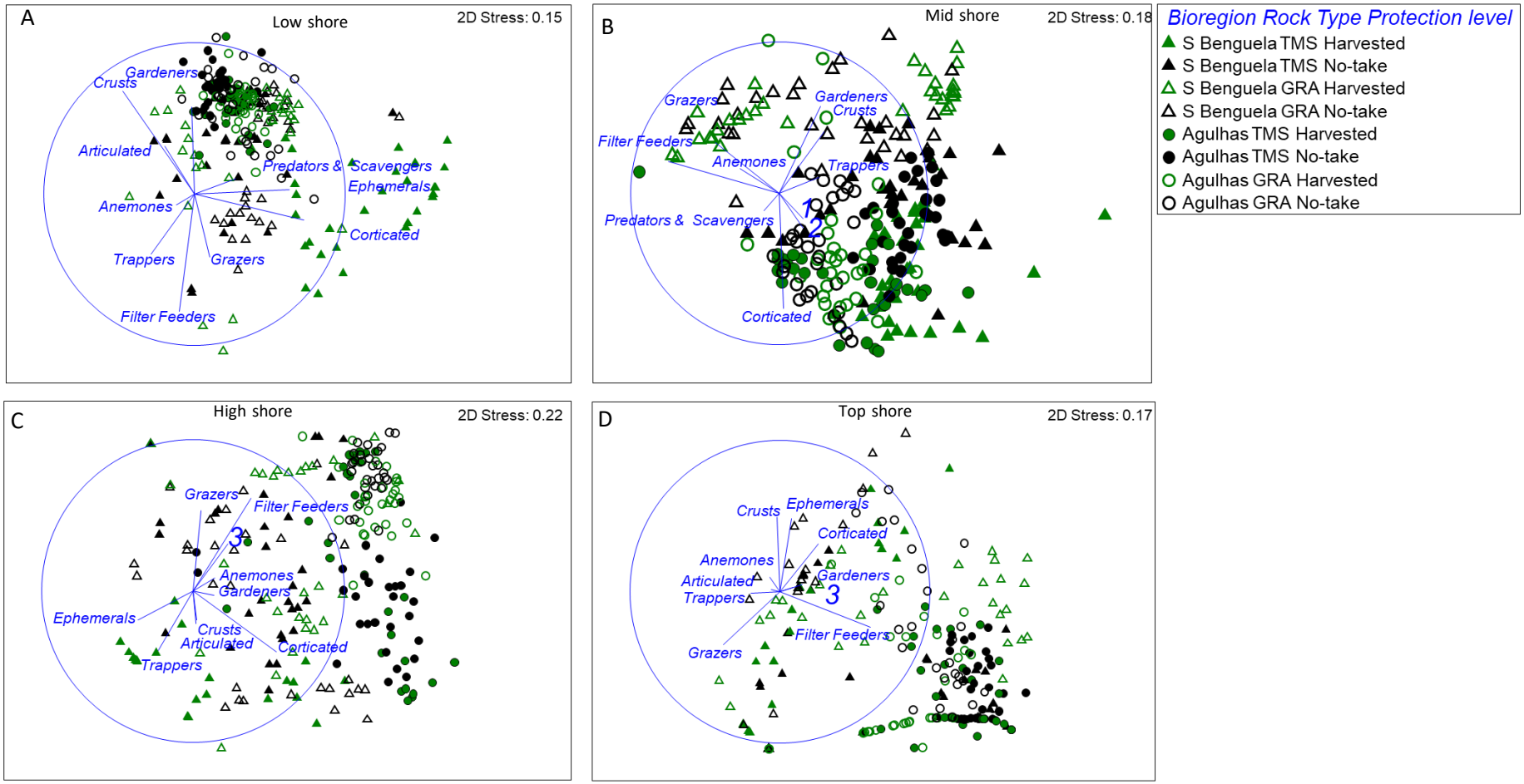



Figure 2.5. MDS plots showing differences in community composition among quadrats that reflect the effects of protection level, ecoregion and rock type for (A) low, (B) mid, (C) high and (D) top shores of 16 sites within Table Mountain National Park MPA, which spans the Southern Benguela (Sn Benguela) and Agulhas ecoregions and features Table Mountain Sandstone (TMS) and Cape Granite (GRA) shores. For clarity, some functional groups are numbered: 1 = Articulated corallines; 2 = Ephemeral algae; 3 = Predators and scavengers.

*Groups distinguishing between harvested and no-take areas*

There were large and significant dissimilarities between no-take and harvested areas at all bar three of the sixteen combinations of region, rock type and shore level that could be compared (Table 2.9). Only in the cases of Southern Benguela granite mid shore, Agulhas sandstone top shore and Agulhas granite mid shore were the differences not significant. SIMPER analysis identified those functional groups that distinguished among no-take and harvested areas.

On the low shore (Fig. 2.6), ephemeral algae were consistently more abundant on harvested shores, most obviously on Southern Benguela sandstone. Corticated algae followed the same pattern, except on Southern Benguela granite. Algal crusts were more prevalent on harvested shores on granite, but not on South Benguela sandstone, and there were no significant differences on Agulhas sandstone. Herbivores – trappers, gardeners and (less obviously) grazers – were more abundant at no-take sites.

Within the mid shore (Fig. 2.7), corticated algae were more abundant on harvested shores (with the exception of Southern Benguela granite), and harvested sites housed larger amounts of ephemeral algae than no-take sites, most obviously on Southern Benguela shores, but also in Agulhas. Algal crusts were, contrary to the low-shore pattern, more abundant on no-take shores, being characteristic and distinguishing members of no-take shores in three cases. Filter feeders also characterised and distinguished no-take sites in three of the four comparisons.

Turning to the high shore (Fig. 2.8), ephemeral algae were yet again prevalent on harvested sites, distinguishing these shores in three of four cases. Corticated algae, however, reversed the trend evident lower on the shore and were more abundant at, and distinguished, no-take sites in two instances. Of the herbivores, trappers (where they were present) were consistently more abundant on no-take shores than harvested shores, and greater grazer abundances were diagnostic of no-take shores in three cases. Filter feeders yielded mixed results, being more abundant on no-take shores in two cases, but less abundant there in the other two cases.

On the top shore (Fig. 2.9) ephemeral algae were more abundant in no-take areas, with one exception; whereas corticated algae remained more common in harvested sites in three out of four cases. Grazers were consistent in reaching greater densities in no-take sites. In three of four instances, filter feeders achieved greater abundance in no-take areas.

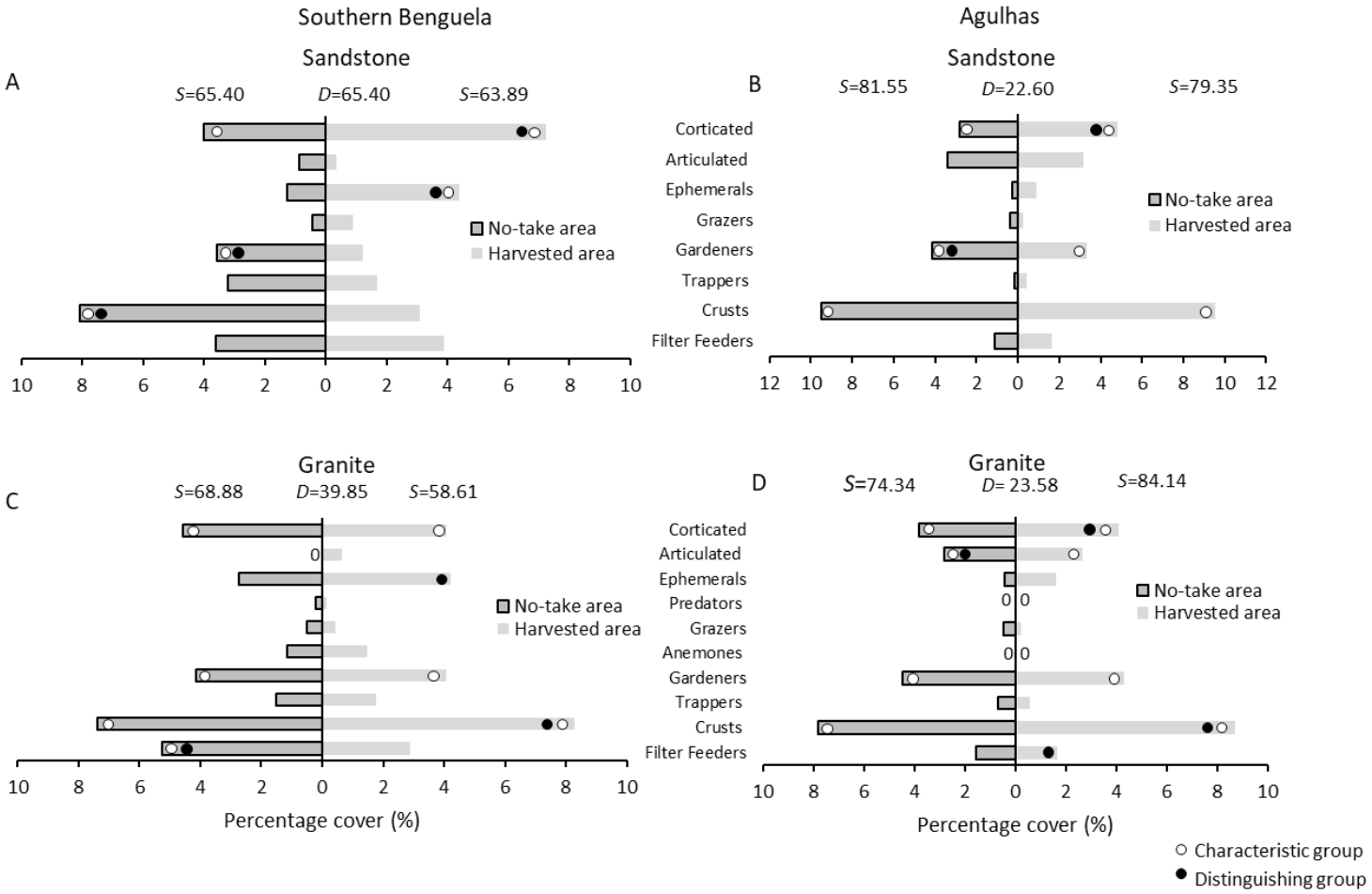



Figure 2.6. Low Shore: Percentage cover of groups responsible for the similarities (*S*) within harvested and no-take areas and the dissimilarities (*D*) between harvested and no-take areas on sandstone in (A) the Southern Benguela and (B) in the Agulhas Ecoregion, and on granite shores in (C) the Southern Benguela and (D) Agulhas. White dots identify groups characteristic of each area; black dots identify groups distinguishing between harvested and no-take areas, with the dots being placed in the sites with greatest abundance; 0 = absence. Units are percentage cover, measured in quadrats of 0.25 $m^2$.

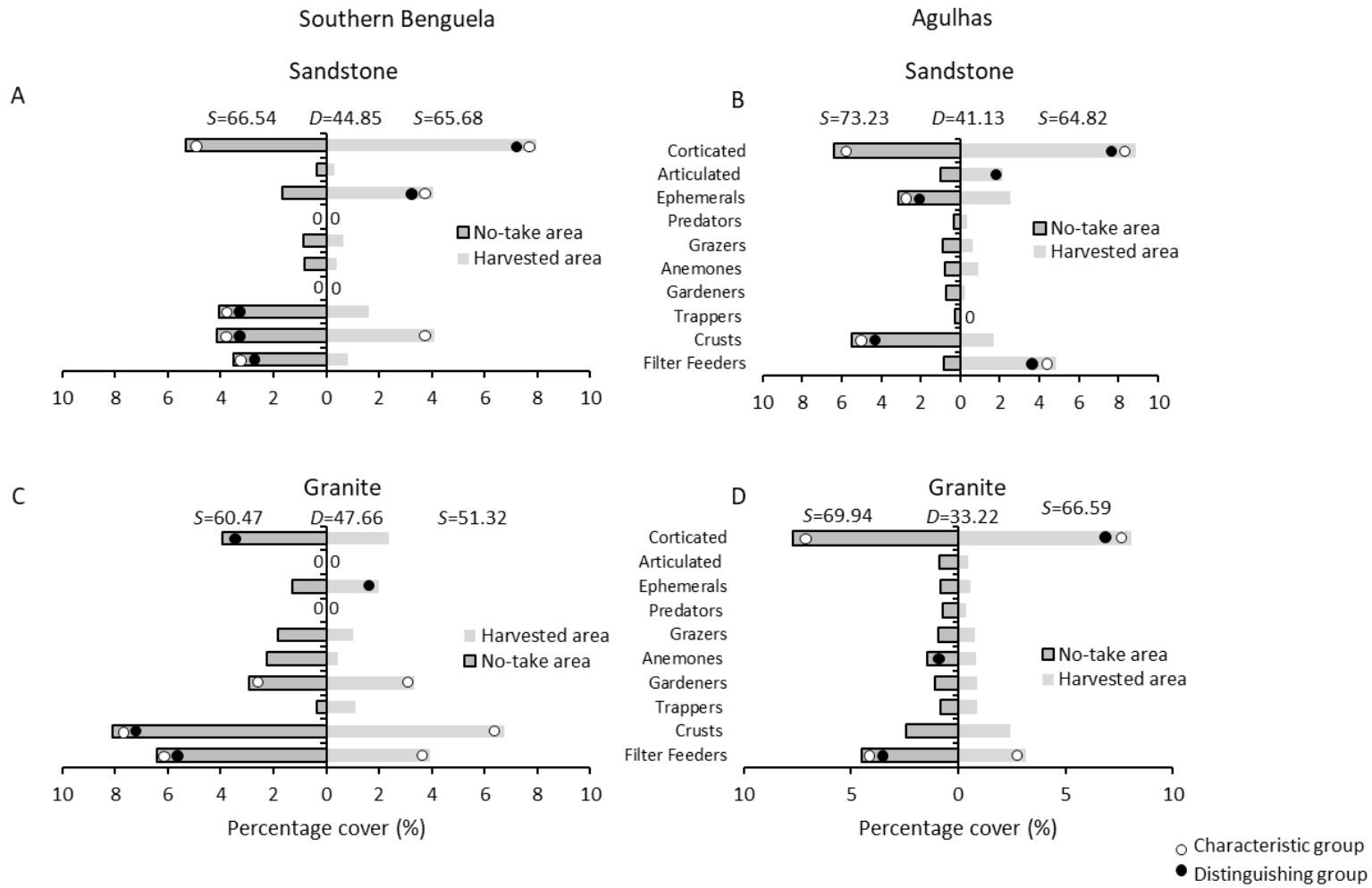



Figure 2.7. Mid shore: Percentage cover of groups responsible for the similarities (*S*) within harvested and no-take areas and the dissimilarities (*D*) between harvested and no-take areas on sandstone in (A) the Southern Benguela and (B) the Agulhas Ecoregion, and on granite shores in (C) the Southern Benguela and (D) Agulhas Ecoregion. See Caption for Fig. 2.6 for further details.

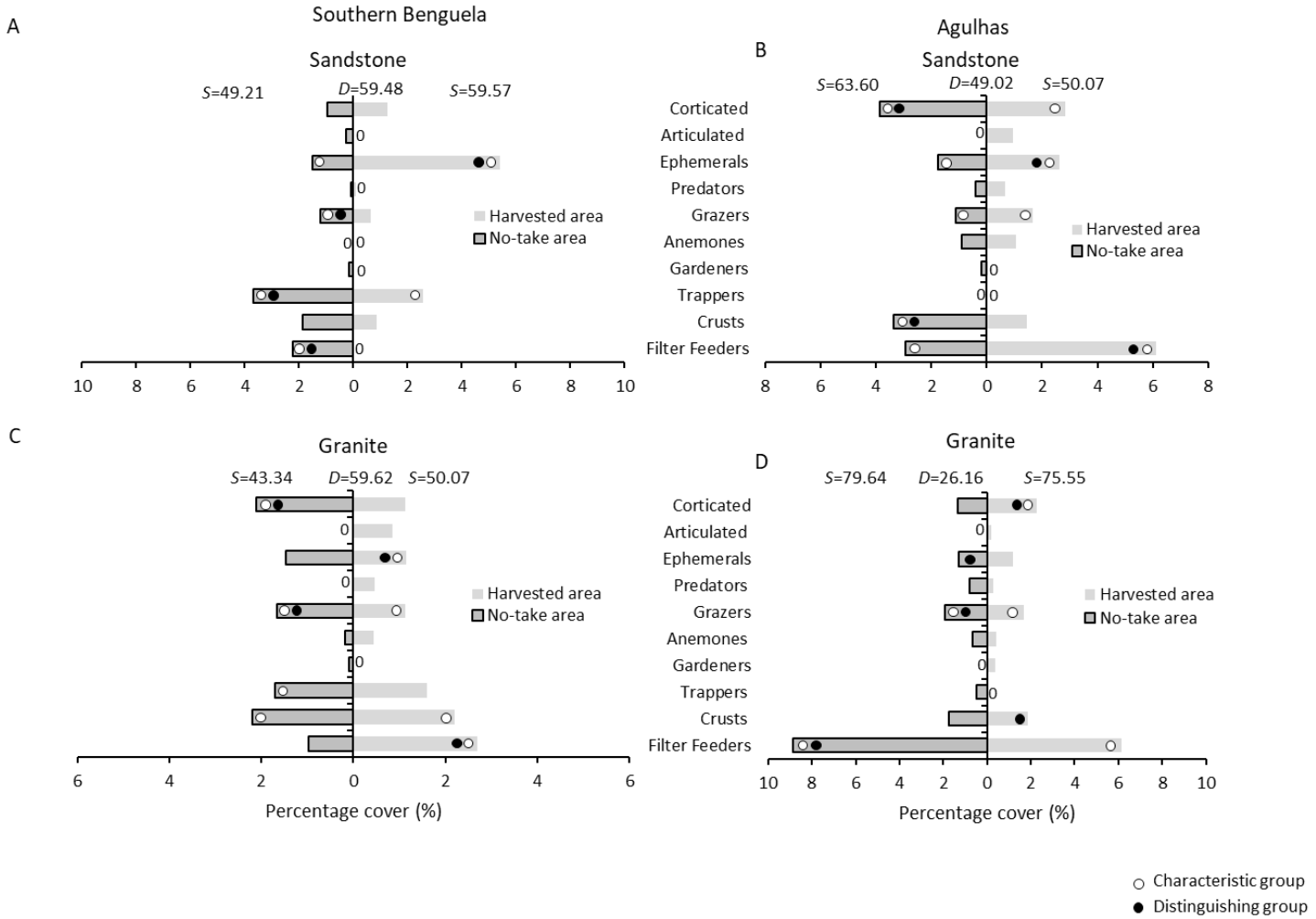



Figure 2.8. High shore: Percentage cover of groups responsible for the similarities (*S*) within harvested and no-take areas and the dissimilarities (*D*) between harvested and no-take areas in the high shore on sandstone in (A) the Southern Benguela and (B) Agulhas Ecoregion, and on granite in (C) the Southern Benguela and (D) Agulhas. See Caption for Fig. 2.6 for other details.

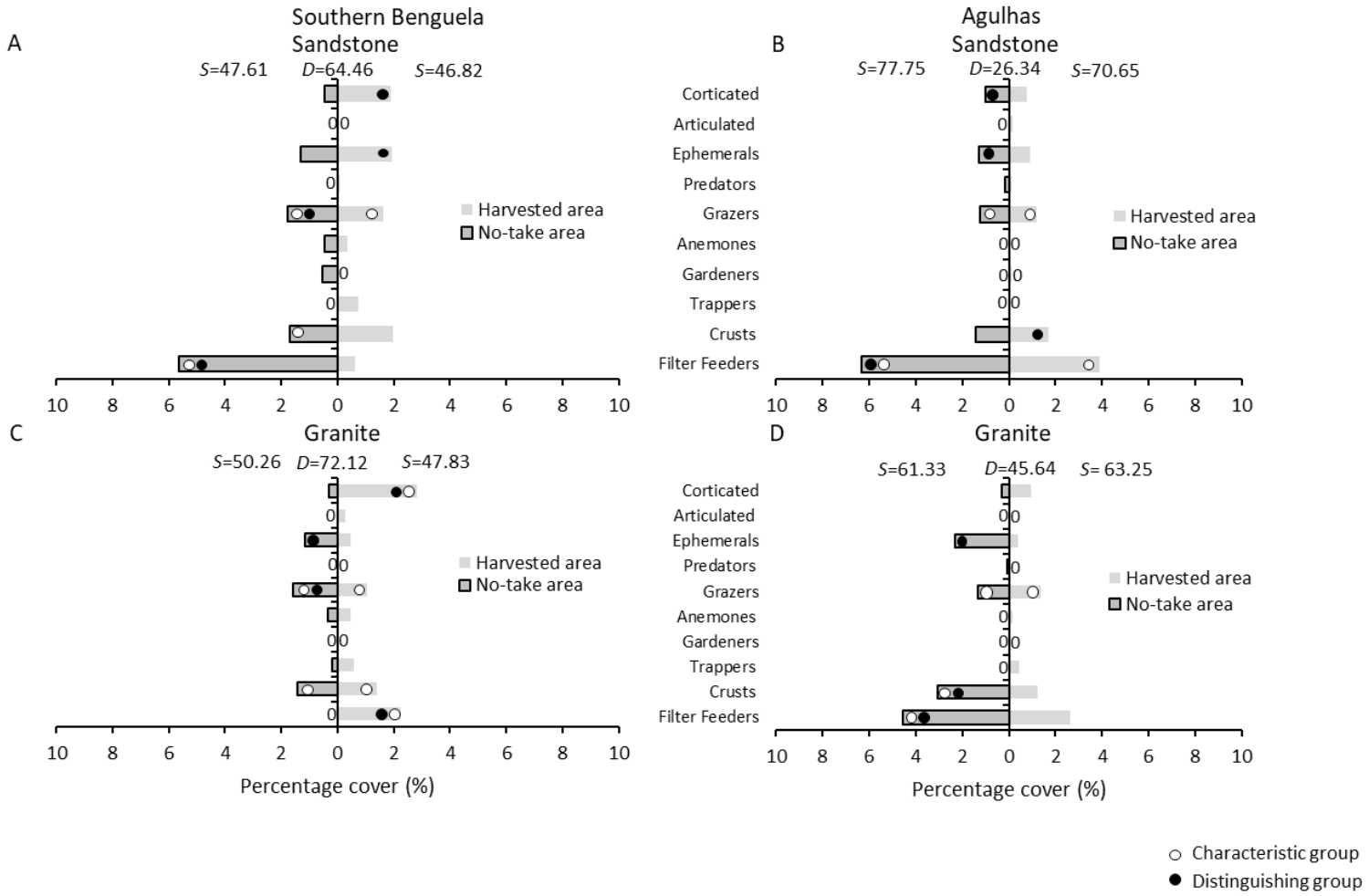



Figure 2.9. Top shore: Percentage cover of groups responsible for the similarities (*S*) within harvested and no-take areas and the dissimilarities (*D*) between harvested and no-take areas, on sandstone in (A) the Southern Benguela and (B) the Agulhas Ecoregion, and on granite in (C) the Southern Benguela and (D) Agulhas Ecoregion. See caption for Fig. 2.6 for further details.

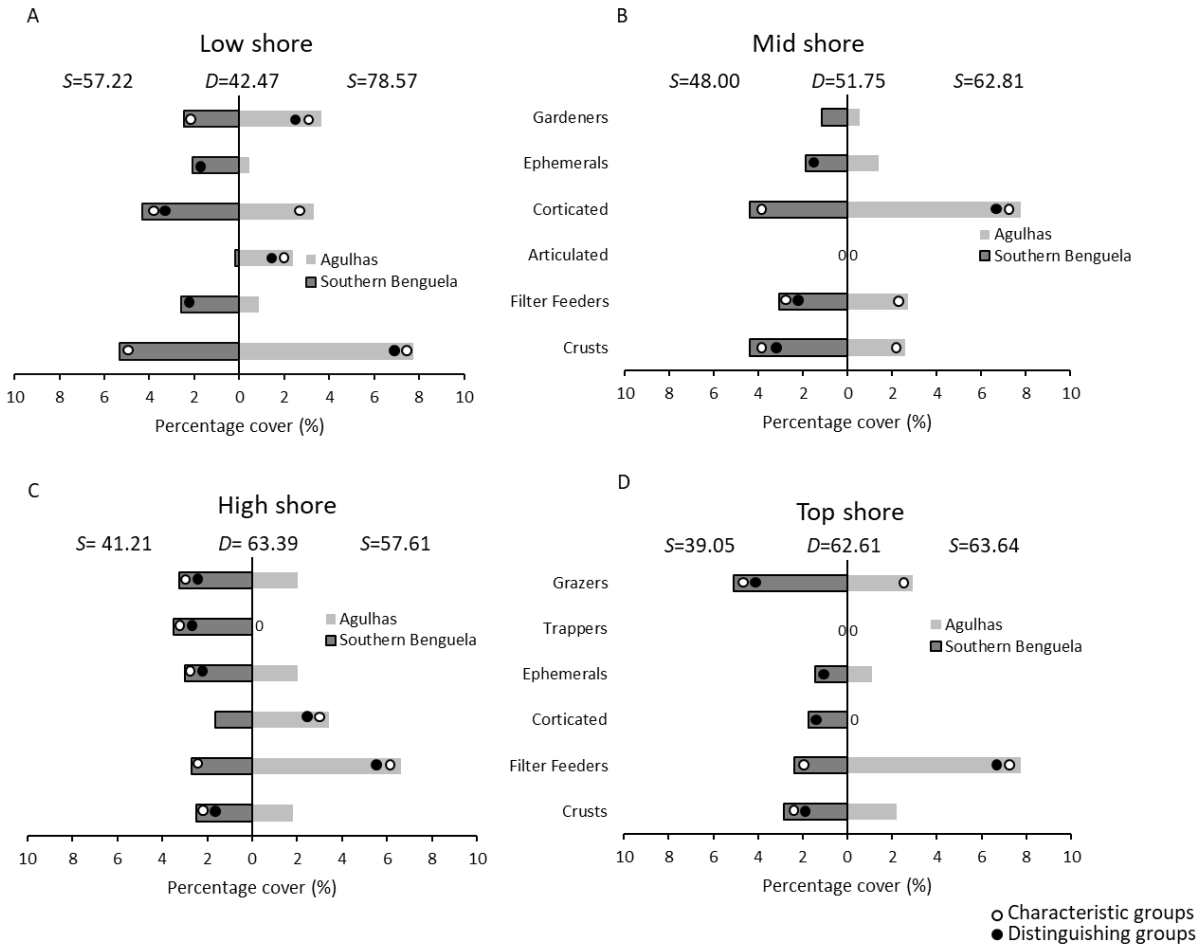



Figure 2.10. Percentage cover of groups responsible for the similarities (*S*) within ecoregions and the dissimilarities (*D*) between ecoregions. White dots identify groups characteristic of each ecoregion; black dots identify groups distinguishing between ecoregions, with the dots being placed in the sites with greatest abundance; 0 = absence. Units are percentage cover, measured in quadrats of 0.25 $m^2$.

*Groups distinguishing ecoregions*

SIMPER identified groups distinguishing ecoregions (Fig. 2.10). Most differences were zone-specific, but ephemeral algae consistently distinguished the Southern Benguela, as did crustose algae in all zones bar the low shore, where they distinguished the Agulhas Ecoregion, associated with a greater abundance of gardening limpets in that zone and region. Grazers were most abundant in high and top zones, where they characterised and distinguished the Southern Benguela. Articulated coralline algae were abundant only in the low shore, where they distinguished and characterised the Agulhas. Corticated algae distinguished the Agulhas in the mid and high shore where their abundance was greatest, but distinguished the Southern Benguela in the low and top zones. Filter feeders reached greatest abundance in the high and top shores, where they distinguished the Southern Benguela, but in the low and mid shores, they distinguished the Agulhas Ecoregion.

## Discussion

Exploitation is a major factor driving communities on intertidal rocky shores, but its impacts vary among rock types and ecoregions (Hockey et al. 1988, Lasiak & Field 1995, Lasiak 1999, Airoldi et al. 2005, Jimenez et al. 2011, 2012, 2015, 2016). The key findings of this study confirmed our hypotheses that shellfish gatherers harvest large individuals of three species of limpets, reducing their densities and mean sizes, and influencing the community composition of rocky shores; but the magnitude of effects of protection were species-specific and depended on ecoregion, rock type and zone. Overall, this study thus confirmed that protection inside no-take areas in the Table Mountain National Park MPA has significant beneficial effects on the commonly harvested invertebrates, but less so (or not at all) on those rarely harvested. As predicted, algal groups also reflected differences in protection levels, likely as a result of altered grazing pressure by removing grazers.

*Selection of species and sizes by harvesters*

Previous studies have demonstrated that shellfish gatherers have preferences for particular species (Durán et al. 1987, Airoldi et al. 2005, Nakin & McQuaid 2014). This leads to a single species, or a few species, dominating the catches (Hockey & Bosman 1986, Durán et al. 1987,

Lasiak 1991b, 1993b, García-Escárzaga et al. 2017). For example, Durán et al. (1987) showed that in Chile shellfish gatherers concentrate their harvest on *Concholepas concholepas* and *Fissurella crassa*. My study revealed that, unlike the east coast of South Africa where the mussel *Perna perna* dominates the catches by shellfish gatherers (Hockey & Bosman 1986, Hockey et al. 1988, Lasiak 1991b, 1992), the limpet *Cymbula granatina* was the most exploited intertidal shellfish in Table Mountain National Park. This could be attributed to its large size, high densities, prevalence on relatively sheltered shores (Eekhout et al. 1992, Bustamante et al. 1995a) and comparatively low strength of attachment (Branch & Marsh 1978). All these characteristics lead to easy access and availability of this species on rocky shores and make it vulnerable to harvesting (Lasiak 1991b). Indeed there is a long history of exploitation of species such as this in southern Africa, extending back at least 100 000 years in the archaeological record (Jerardino et al. 2008, Parkington et al. 2013, Will et al. 2016, García-Escárzaga et al. 2017). *Cymbula oculus* was also harvested at three Southern Benguela sites, but in smaller amounts, reflecting the fact that its densities there are lower than those of *C. granatina*. By contrast, *Scutellastra argenvillei*, which inhabits semi-exposed to exposed areas (Branch & Steffani 2004), was recorded as being harvested at only one site, and only on one occasion. On the other hand, the absence of *S. longicosta, S. cochlear* and *S. granularis* from any catch records supports the view that these three species are rarely harvested in the region I worked, and that harvesting is highly selective (see Hockey et al. 1988, Nakin et al. 2012, Nakin & McQuaid 2014, 2016 for records of harvesting elsewhere on the coast).

The larger shell lengths of *C. granatina* and *S. argenvillei* individuals collected by shellfish gatherers compared to those in the natural populations upholds my first hypothesis to this effect, and supports other findings that shellfish gatherers target large individuals (Durán et al. 1987, Lasiak 1991b, 1992, Mannino & Thomas 2001, Jimenez et al. 2011, Alexander & Gladstone 2012). This usually leads to reductions in the mean sizes of the individuals in the natural populations (Eekhout et al. 1992, Jimenez et al. 2011).

### *Densities of key species*

Exclusion of shellfish gatherers from MPAs often leads to greater densities of commonly harvested species inside no-take areas relative to harvested areas (Moreno et al. 1984, 1986, Hockey & Bosman 1986, Hockey et al. 1988, Edgar & Barrett 1999, Alexander & Gladstone

2012, Bednar & Trulio 2017). For example, higher densities of the limpet *Cellana tramoserica* were found in the Bouddi National Park Marine Extension relative to unprotected shores (Alexander & Gladstone 2012). The same was true for *Patella ulyssiponensis* in La Palma MPA (López et al. 2012), for *Cymbula oculus* in Dwesa Nature Reserve in South Africa (Branch & Odendaal 2003), and for *Fissurella picta* and *Fissurella limbata* in the Marine Reserve of Mehuin in Chile (Duarte et al. 1996). These increased densities were all attributed to protection providing a refuge for the target species. My results produced similar patterns on sandstone (but not on granite, where densities were low overall) for the commonly harvested limpets *C. granatina, C. oculus* and *S. argenvillei*, which indicates that effective protection yields greater limpet densities.

This conclusion is further strengthened by the fact that the rarely harvested limpets *S. granularis*, S. *longicosta* and *S. cochlear* had equivalent densities at both protection levels in most instances (six out of ten comparisons). For *S. longicosta*, no differences in density existed inside and outside no-take areas. For the other two species, there were, however, exceptions to this pattern. For *S. cochlear*, densities inside and outside no-take MPAs were the same in two cases, greater in no-take areas in one case, and greater in harvested areas in one case. *Scutellastra granularis* attained high densities inside no-take areas in the Southern Benguela (but not in the Agulhas Ecoregion, where densities were equivalent at the two levels of protection). It is possible that the greater abundance of *S. granularis* in no-take areas in the Southern Benguela was due to facilitation of this limpet's densities by *M. galloprovincialis* (Griffiths et al. 1992, Branch et al. 2008, 2010), as this mussel is more abundant at protected sites in the Southern Benguela, but more scarce in the Agulhas Ecoregion. In the Agulhas Ecoregion, *S. granularis* density is often restricted by barnacles such as *Tetraclita serrata* and *Chthamalus dentatus* (Branch 1976, Nakin & McQuaid 2014), which are not harvested and occurred at equivalent densities at both protection levels in that region. Whatever the explanation, there were significant and complex interactions among ecoregion, rock types and protection level for *S. granularis* and *S. cochlear* as a result of these variable outcomes, which was not unexpected in absence of a direct effect of protection by the MPA. The absence or inconsistent outcomes of any protection effect observed for rarely harvested species also concurs with previous studies, e.g. another rarely harvested species, *Cellana capensis*, had higher densities in harvested than no-take areas on the southeast coast of South Africa (Lasiak 1993a).

Protection is, however, not always effective. An absence of any protection effect was reported by Nakin & McQuaid (2014) for limpets in Dwesa Nature Reserve, attributable to poaching in the reserve and differences in the intensity of harvesting outside the reserve. Similarly, Coppa et al. (2012, 2015) associated the decline of *Patella ferruginea* in Italy's Mal di Ventre MPA with poaching and ineffective enforcement of regulations. Although *C. oculus* had high densities inside sandstone no-take areas, its populations appear to have dramatically decreased in the TMNP MPA from 12.35 $m^{-2}$ to 8 $m^{-2}$ (Maneveldt et al. 2009). The lack of protection effect on the granite rocky shore might be due to higher mortality associated with dislodgement of limpets on the rock, as it has been suggested that they cannot attach as firmly to this rock type (McQuaid et al. 1985). Greater natural mortality on the granite rocky shores might reduce the densities of this species, although there was no indication of this being reflected in smaller sizes on granite shores. Nevertheless, low densities of *C. oculus* on granite rocky shores may not reflect a failure of protection inside no-take areas of the MPA, but rather an influence of habitat type on the density of the species.

I had anticipated that there would be differences in the abundances of limpets between the two ecoregions sampled in this study. This manifested itself in two ways. First, some species were either confined to, or substantially more abundant, in one of the two ecoregions. That was the case for *C. granatina* and *S. argenvillei* (predominantly Southern Benguela), and *C. oculus* and *S. longicosta* (predominantly Agulhas). For those species that occurred in both ecoregions, I had suspected that there might be greater abundances in the Southern Benguela than the Agulhas Ecoregion because of the greater productivity on the west coast and the fact that greater biomasses of grazers have been recorded there (Bustamante et al. 1995b). That was, however, not the case. Differences in mean abundances of *S. granularis* were non-significant in three of four comparisons, and those for *S. cochlear* conformed to my hypothesis on only two of four cases. The densities of *S. longicosta* that I recorded were magnitudes less than those recorded in Dwesa Nature Reserve (Nakin & McQuaid 2014). This might reflect that the species is reaching the western limit of its distribution range in the TMNP, resulting in low densities (Hidas et al. 2010).

*Sizes of key species*

For the two commonly harvested species for which I have size data of collections by harvesters, i.e. *Cymbula granatina* and *Scutellastra argenvillei*, harvesting focussed specifically on large individuals. Shellfish gatherers generally target large individuals, which can truncate the size distribution of populations in harvested areas (Branch & Odendaal 2003, Sagarin et al. 2007, Jimenez et al. 2011, Alexander & Gladstone 2012, Coppa et al. 2012, 2015, Fenberg et al. 2012, Bednar & Trulio 2017), as has been reported for *Cymbula oculus* (Branch & Odendaal 2003), *Cellana capensis* (Lasiak 1993a), *Lottia gigantea* (Sagarin et al. 2007, Lucas & Smith 2016), and many other species, including fish (Keough et al. 1993, Marra et al.2017, Heyns-Veale et al. 2019).

In my results, harvesting had variable effects on the sizes of key species. The most frequently harvested species, *C. granatina*, consistently had larger sizes inside protected vs. harvested areas, on both sandstone and granite rocks. The second frequently harvested species, *Scutellastra argenvillei*, yielded the same outcome on sandstone, but not on granite, possibly because densities there were much lower, and no harvesting of this species was recorded at sites with granite rocks. However, *C. oculus*, which is also harvested, displayed a weak effect of protection on size, being larger outside no-take areas than inside on sandstone, and not significantly different on granite. Effects of protection may thus be species-specific, habitat-specific and region-specific (Nakin & McQuaid 2014). The presence of larger individuals in no-take areas is most likely a result of greater survival of limpets there, associated with a reduction in harvesting mortality (Branch & Odendaal 2003, Nakin et al. 2012, Lucas & Smith 2016, Zarrouk et al. 2016, Bednar & Trulio 2017). The existence of larger individuals in protected areas enhances reproductive output because of their greater fecundity (Branch & Odendaal 2003, Orozco et al. 2013, Zarrouk et al. 2016). For species like *C. oculus*, which are protandric hermaphrodites that undergo a sex change from male to female at an intermediate size (age), a reduction of mean size could also affect the reproductive success as it will skew sex ratios (Branch & Odendaal 2003).

In contrast to the three harvested species of limpets, all three rarely harvested species, *S. longicosta*, *S. granularis* and *S. cochlear*, conformed to expectation and showed either no effects or no consistent effects of protection on their mean sizes. The size of *S. longicosta* was

not related to the level of harvesting, and the same was true in three of the four comparisons possible for *S. cochlear*, although in the fourth comparison (Agulhas granite), sizes were greater in harvested than fully protected areas. For *S. granularis*, size was always larger at harvested sites, but only significantly so in two of the four cases. Similar findings were reported for *S. granularis* at Dwesa Nature Reserve, with larger sizes outside than inside the reserve (Nakin & McQuaid 2014). The occurrence of larger individuals in harvested areas may reflect reduced competition due to the removal of harvested species, although that has not yet been demonstrated empirically. Lasiak & White (1993) have, however, shown that high densities of the limpet *Cellana capensis* reduce microalgal availability, with implied competitive effects for other species.

### *Community composition*

There were considerable differences in community composition between the harvested and no-take areas. These differences reflect effective protection of communities which led to increases in the abundance of filter feeders, grazers and trappers inside no-take areas, while these groups were reduced in the harvested areas. Reductions of these taxa in harvested areas have frequently been reported by others (Moreno et al. 1984, Hockey & Bosman 1986, Hockey et al. 1988, Lasiak & White 1993, Dye 1993, 1995, Lasiak & Field 1995, Sharpe & Keough 1998, Lasiak 1998, 1999, Moreno 2001, Ceccherelli et al. 2005, 2006, 2011, Sink et al. 2010, Barbiero et al. 2011). Their depletion at harvested sites could have promoted the abundances of algae due to diminishment of grazing pressure and/or competition for space. Similar findings have been reported for Dwesa-Cwebe, Hluleka and Mkambati Nature Reserves, and in Tsitsikamma MPA, on the east and south coasts of South Africa respectively, where community compositions inside these protected areas have been shown to be dominated by commonly harvested species such as *Perna perna*, *Haliotis spadicea*, *Scutellastra barbara*, *Cymbula oculus* and *Cymbula miniata* (Hockey & Bosman 1986, Lasiak & Field 1995, Dye 1998, Lasiak 1998, 1999, Hanekom 2011). Comparable outcomes have been noted worldwide: Barrett et al. (2009) reported that the commonly harvested urchin *Heliocidaris erythrogramma* is a characteristic and distinguishing taxon for no-take areas in Tasmanian marine reserves; Jimenez et al. (2015, 2016) documented that three commonly harvested taxa, *Tridacna* spp., *Trochus niloticus* and *Turbo* spp., were the major groups distinguishing between the communities of protected and no-take areas in New Caledonia. The fact that commonly

harvested filter feeders, grazers and trappers were the major functional groups distinguishing between harvested and no-take areas in my data strengthens my conclusion that protection influenced the community composition, as reflected in other studies (Lasiak & Field 1995, Lasiak 1998, 1999, Barrett et al. 2009, Jimenez et al. 2016). Protection in no-take areas often results in a mosaic of communities, with patches of filter feeders, grazers and trappers, while adjacent harvested areas tend to have extensive uniform mats of algae, as described for Dwesa-Cwebe and Hluleka Nature Reserves and Tsitsikamma MPA (Hockey & Bosman 1986, Lasiak & Field 1995, Dye 1998, Lasiak 1998, Hanekom 2011).

Whilst not the primary focus of this study, the differences in community composition also reflected the consistent and significant influence of ecoregion, which led to frequent interactive effects between protection and ecoregion. My results are in agreement with the biogeographic findings of Emanuel et al. (1992), Bustamante et al. (1995b) and Bustamante & Branch (1996a) that community composition changes among ecoregions. These differences are associated with dissimilarities in nutrient availability and temperature, with the Southern Benguela having higher nutrient availability and cooler waters than the Agulhas (McQuaid et al. 1985, Emanuel et al. 1992, Bustamante et al. 1995b). The Southern Benguela displayed higher abundances of ephemeral algae, grazers and trappers, probably as a result of higher nutrient availability associated with upwelling (Bustamante et al. 1995b, Bustamante & Branch 1996a).

The presence of larger quantities of algal crusts inside no-take areas probably reflects trophic cascades and competitive interactions among functional groups, since this group has been shown to positively respond to the presence of abundant grazers, which deplete macroalgae (Blamey & Branch 2009) that would otherwise overgrow crusts. Harvested areas frequently had the highest percentage cover of corticated and ephemeral algae, which signals an altered community composition with lower levels of grazers being less able to control algal growth in harvested areas (Bustamante et al. 1997, Lasiak 1998, Barbiero et al. 2011). These responses are not surprising given that changes in community composition following protection from harvesting are expected to occur within five years of protection (Durán & Castilla 1989, Ceccherelli et al. 2005, 2006, Coleman et al. 2015, Ferreira et al. 2017).

The lack of protection effects on the community composition in the top and mid shores in some instances (Southern Benguela mid shore granite, Agulhas mid shore granite and top shore sandstone) may be associated with the fact that rarely harvested groups, such as barnacles and

the limpet *S. granularis*, dominate these zones. In particular, mid shore granite rock ledges were rarely inhabited by most limpets and, as a result, community composition in this zone – at both protection levels – was dominated by corticated algae, as McQuaid & Branch (1985) have noted previously. The scarcity of taxa susceptible to harvesting on this rock type nullifies the role of protection because little harvesting occurs there.

Although PERMANOVA detected significant differences between harvested and no-take areas in both the Southern Benguela and Agulhas ecoregions, MDS did not display clear-cut separation of community composition between protection levels in the Agulhas Ecoregion, and SIMPER indicated relatively low dissimilarities between harvested and no-take areas (22.6–49.0%). The average levels of similarity (70.9%) in the Agulhas Ecoregion were equivalent to those recorded for converged communities (Sink et al. 2010, Jimenez et al. 2012). In addition, both protection levels were characterised by similar functional groups and dominated by algae, which are usually typical of areas experiencing high harvesting pressure (Hockey & Bosman 1986, Lasiak & Field 1995, Lasiak 1998, Barrett et al. 2009, Sink et al. 2010). Thus, the dominance of some groups of algae in no-take areas in the Agulhas Ecoregion contradicts early findings in other MPAs along the south and east coasts of South Africa, e.g. Dwesa, Hluleka and Mkambati Nature Reserves (Hockey & Bosman 1986, Lasiak & Field 1995, Lasiak 1998) and Tsitsikamma MPA (Hanekom 2011), where commonly harvested consumers dominate and characterise no-take areas, with algae being less abundant (Lasiak & Field 1995, Lasiak 1998, Hanekom 2011). This may, however reflect the influence of upwelling in the Table Mountain National Park MPA, which supplies nutrients and thus facilitates algal growth and productivity, while the contrary findings were from more oligotrophic regions of the country, where grazing may have a more severe effect on algal abundances.

In the Southern Benguela Ecoregion, differences between harvested and no-take areas were more obvious ($D$ = 39.85–72.12%), reflecting greater divergence (Sink et al. 2010, Jimenez et al. 2012) than in the Agulhas Ecoregion. There, communities reflected conventional expectations to a much greater degree, especially on sandstone shores, where corticated and ephemeral algae were prevalent in harvested situations, associated with the depletion of herbivores.

In terms of individual species, one striking absentee from the list of characteristic species of the Agulhas Ecoregion was the indigenous brown mussel *Perna perna*, which was abundant in

False Bay (at the southeast limits of the Agulhas Ecoregion) in the 1980s, but had diminished by 2011 (Griffiths & Mead 2011, Reimers et al. 2014); and which I failed to record in my samples. Changes in its abundance and presence in this region are likely associated with cooling of the waters and a southeasterly contraction of this species' range (Pfaff et al. 2019). Replacing it, the alien Mediterranean mussel *Mytilus galloprovincialis* has become a dominant element of all the shores I examined, and featured in the temporal changes in community composition that I address in the following chapter.

## Conclusions

Shellfish gatherers in Table Mountain National Park collected mainly the limpets *C. granatina, C. oculus* and *S. argenvillei*, as well as mussels, and targeted large individuals of the three limpet species, supporting my first hypothesis to this effect. Focused harvesting of large individuals was associated with low densities and small sizes of those species of limpets in the harvested areas.

My second hypothesis, that protection would result in high densities and sizes of harvested limpets inside no-take areas, was supported on sandstone shores, but not on granite rocky shores where densities of commonly harvested species were lower and similar between harvested and no-take areas, possibly because granite rocks are unfavourable for the attachment of limpets, rendering their densities relatively low there.

Also gaining qualified support was my third hypothesis, that rarely harvested species would not show differences in densities and sizes that could be related to protection level: *S. longicosta* conformed to the hypothesis, whereas *S. granularis* provided only weak or no support; *S. cochlear* yielded sizes that were larger in harvested than no-take areas, and its densities were ambivalent with respect to protection. Collectively, the failure of non-harvested species to respond to differences in protection levels supports the idea that harvesting is responsible for the observed differences in the abundances of harvested species between the two levels of protection.

Differences in protection did affect rocky shore community composition, supporting my fourth hypothesis. The depletion of limpets that were grazers and trappers, and of filter feeders, was

associated with dramatic increases in algal domination of the community composition in the harvested areas of Southern Benguela sandstone shores. This further resulted in a reduction in algal crusts, which tend to be positively associated with limpets. By contrast, in the equivalent no-take areas, grazers, trappers and filter feeders dominated the community composition. This pattern was, however, not clearly evident on granite shores or in the Agulhas Ecoregion. Effects of harvesting on community composition were thus specific to region, zone and rock type. Likely causes of these differences include (a) differences in the intensity of harvesting in different areas; (b) targeting of different species; (c) effectiveness of enforcement of protection, (d) differences in abundance between different rock types. Influences of protection were thus most clear for sandstone rocks in the Southern Benguela, where harvesting was concentrated and target species most abundant.

The sizes and densities of key limpet species might have been forecast to be greater in the Southern Benguela than the Agulhas Ecoregion because of greater productivity there as a result of upwelling (Bustamante et al. 1995b). This was, however, not the case. Yet, striking differences in community composition between ecoregions did emerge, despite the fact that analyses were based on functional groups and not at species level.

In the following chapter I pursue a more detailed comparison of selected Southern Benguela sandstone shores to examine the effects of both harvesting and the arrival of the alien mussel *Mytilus galloprovincialis*, based on spatial and long-term temporal comparisons of five shores.

# Chapter 3: Effects of harvesting and an invasive mussel on intertidal rocky shore communities based on historical and spatial comparisons


## Abstract

Intertidal rocky shores are the most accessible marine habitats and therefore heavily impacted by harvesting pressures. In recent years, these ecosystems have also been increasingly invaded by alien species, which further confounds the effects of harvesting on rocky shore community structure and functioning. Recent survey data, combined with historical data from 1970, were used to assess temporal changes over the intervening period in rocky shore communities at two sites (Wireless Point and Wireless Island) where harvesting has increased over the last two decades. Three kinds of changes emerged: (1) the appearance of alien species; (2) the effects of increased harvesting pressure; and (3) the direct and indirect effects of these changes on other species. A striking result was transformation of mid-shore zones on exposed shores by the appearance of the invasive Mediterranean mussel *Mytilus galloprovincialis*, and the indirect effects of this on the demography and vertical zonation patterns of the granular limpet *Scutellastra granularis*. Adult limpets have been excluded by the mussel, whereas juveniles find a secondary home on the shells of the mussel. To further disentangle the effects of harvesting from those of alien invasions, a spatial comparison was made between two currently unharvested no-take areas (at Scarborough South and Scarborough North) and two regularly harvested sites (Kommetjie and Wireless Point). Harvesting has decimated granite limpets *Cymbula granatina* and Argenville's limpets *Scutellastra argenvillei.* This has led to the proliferation of opportunistic seaweeds, such as *Ulva* spp. The dual effects of alien invasive species and over-harvesting have major ecosystem effects but do not necessarily diminish biodiversity because alternative habitats have developed that provide opportunities for colonisation by additional species.


## Introduction

Harvesting of rocky shore organisms has intensified in South Africa and elsewhere in recent decades due to increased human population density associated with development of residential settlements and the concentration of people in and around urban areas, coupled with crop failures in some years (Branch 1975a, Eekhout et al. 1992, Keough et al. 1993, Addessi 1994, Griffiths & Branch 1997, Moreno 2001, Jimenez et al. 2011, 2015, 2016, Lucas & Smith 2016). These conditions have led to increased subsistence/recreational harvesting and poaching of intertidal and shallow-water organisms (Addessi 1994, Griffiths & Branch 1997, Moreno 2001, Raemaekers et al. 2011, Jimenez et al. 2011, 2015, Marra et al. 2017). As a result, there is concern that overharvesting is a major threat to rocky shores adjacent to coastal residential

areas (van Herwerden et al. 1989, Addison et al. 2008). This increased disturbance is likely to reduce densities of harvested species, and alter population structure and community composition on rocky shores (Lasiak 1993a, 2006, Addessi 1994, Lasiak & Field 1995, Moreno 2001, Branch & Odendaal 2003). To devise appropriate management measures and evaluate effectiveness of current strategies (e.g. Marine Protected Areas - MPAs) authorities need information about the impacts of disturbance and protection of rocky shore fauna and flora (Lasiak & Field 1995, Lasiak 2006, Jimenez et al. 2011, 2012, 2015, 2016, Nakin & McQuaid 2016, Marra et al. 2017).

Historical changes in small-scale fishing activities have been linked with both direct and indirect changes in rocky shore populations and communities (Branch 1975a, Duarte et al. 1996, Bednar & Trulio 2017, Wilson-Brodie et al. 2017). The direct impacts include declines in the density of harvested species such as *Helcion concolor* (Branch 1975a). Following the provision of protection inside MPAs in Chile, densities of previously intensely harvested species, e.g. *Fissurella picta* and *Fissurella limbata* (Duarte et al. 1996) and *Concholepas concholepas* (Castilla & Durán 1985, Manríquez & Castilla 2001) gradually increased over time. Harvesting often also reduces the sizes of target species, as has been demonstrated for the limpet *Cymbula oculus* (Branch & Odendaal 2003), a second limpet *Lottia gigantea*, and the winkle *Tegula funebralis* (Kido & Murray 2003, Bednar & Trulio 2017); whereas sizes of rarely harvested species are usually unaffected by harvesting. There are exceptions, however. For example, the whelk *Nucella lapillus* has been shown to increase in size in the face of harvesting directed at other species (Fisher et al. 2009), or to decline in size, due to the indirect effects of harvesting the mussel *Mytilus edulis*, one of the main food sources for *N. lapillus* (Wilson-Brodie et al. 2017). Increased harvesting can also change the entire composition and functioning of rocky shore communities (Branch 1975a, Lasiak & Field 1995).

Apart from harvesting, rocky shores in South Africa and worldwide have been invaded by alien species. Consequently, community composition, and the abundances and sizes of various indigenous species, have been altered (Roy et al. 2003, Robinson et al. 2007, 2016, Branch et al. 2008, 2010, Reimers et al. 2014, Alexander et al. 2015, Sadchatheeswaran et al. 2015). The most notable of these aliens is *Mytilus galloprovincialis*, a known global invasive species that was first recorded in South Africa in 1979 and has since rapidly spread from the west coast to the south coast and invaded semi-exposed and wave-exposed areas, where it forms dense

mussel beds (Branch et al. 2008, 2010). It out-competes most indigenous species such as *Aulacomya atra*, *Scutellastra argenvillei*, *Scutellastra granularis*, *Gunnarea gaimardi* and *Perna perna* (Steffani & Branch 2005, Robinson et al. 2007, Branch et al. 2008, Rius & McQuaid 2009, Sadchatheeswaran et al. 2015). The invasion by *M. galloprovincialis* led to a reduction in density of adults and recruits of *A. atra*, *G. gaimardi* and *S. granularis* on the primary substrate in semi-exposed and exposed areas (Branch et al. 2008, 2010). However, invasive species do not always competitively exclude other species, since they also comprise a secondary substratum for epibiotic growth (e.g. Miyamoto & Noda 2004). By increasing habitat complexity, mussels act as ecosystem engineers that can facilitate the survival of other, smaller, organisms that take advantage of the shelter from waves and predators provided by the dense mussel bed (Gutiérrez et al. 2003). Arrival of *M. galloprovincialis* has, for example, led to an overall increase in densities of the limpet *S. granularis* in zones dominated by the mussel because it provides a favourable substratum for the limpet's juveniles (Hockey & van Erkom Schurink 1992, Branch et al. 2010), but has also decreased the mean size of *S. granularis* (Griffiths et al. 1992). While species-specific effects of interactions with *M. galloprovincialis* have been well documented, the influence of *M. galloprovincialis* on community composition has received less attention (Robinson et al. 2007, Sadchatheeswaran et al. 2015).

The aim of this study was to assess the effects of harvesting and the invasive alien mussel *Mytilus galloprovincialis*, both of which have dramatically increased since the 1970s, on rocky-shore biodiversity on selected shores in the Table Mountain National Park Marine Protected Area (hereafter referred to as TMNP MPA). Two comparisons were made: (1) between historical data gathered in 1970 and my 2017 surveys, which were compared at two sites (Wireless Point, which is accessible and intensely harvested, and Wireless Island, which is less accessible but also harvested), to reveal temporal changes attributable to intensification of harvesting and the arrival of the alien mussel *Mytilus galloprovincialis*; (2) spatial comparisons based on my 2017 data for four sites, including two in a 'no-take' MPA (Scarborough North and South), and two that are accessible and experience intense harvesting (Wireless Point and Kommetjie).

Four hypotheses were tested: (1) Based on the increase in human populations along the coast, densities and sizes of highly harvested *Cymbula granatina* and *Scutellastra argenvillei* will have declined from those recorded in the past, while those of the rarely harvested *Scutellastra*

*granularis* will have changed due to the invasion by the alien mussel, *M. galloprovincialis*. Specifically, declines attributed to harvesting were expected to be higher at the easily accessed sites than at the less accessible site. (2) Arising from the impacts of *M. galloprovincialis* cited above, sizes, densities and the vertical zonation pattern of *S. granularis* will have changed from the past, following the arrival of *M. galloprovincialis* at Wireless Island. (3) The community composition of Wireless Island and Wireless Point would have been altered over time by both the arrival of the alien and by harvesting in the area. (4) The present-day community composition will differ among sites as a result of a difference in harvesting pressure between areas inside and outside no-take areas of the TMNP MPA. (5) Densities and shell lengths will also differ among sites because of differences in protection level, with the expectation that they will be greater for harvested species at sites that are fully protected. By assessing the cumulative effects of harvesting and introduced species on rocky shores, this study provides valuable information regarding the effectiveness of the TMNP no-take sections of the MPA in terms of protecting exploited stocks and coastal biodiversity.

## Materials and methods

### *Study area and sites*

This study was conducted in the Table Mountain National Park Marine Protected Area (TMNP MPA) on the coast of the Cape Peninsula, South Africa (Fig. 3.1). The TMNP MPA was proclaimed in 2004 and is situated in the transition zone between the Agulhas and Southern Benguela ecoregions (Tunley 2009, Sink et al. 2012, 2019), with this study being positioned in the latter, on the west coast of the Cape Peninsula. This part of the MPA has two restricted (no-take) areas, namely Cape of Good Hope and Karbonkelberg, which alternate with controlled-use zones (where harvesting is permitted within laws limiting activities). The restricted areas cover a variety of rocky-shore habitats that differ in substrate type – most commonly Table Mountain Sandstone and Cape Granite. For the purpose of this chapter, however, comparisons were restricted to sandstone sites.

Five study sites were selected: (i) Kommetjie and Wireless Point, which are heavily harvested and fall in controlled-use areas of the MPA, (ii) Wireless Island, also in a controlled-use area, but less frequently harvested because it is less accessible, lying on an emergent reef ca. 25 m

offshore from Wireless Point, and (iii) Scarborough North and South, two sites in the Cape of Good Hope no-take area, which are ca. 200 m apart.

The sites were used for different purposes. Wireless Island and Wireless Point were employed to make temporal comparisons between 1970 and 2017. Wireless Point and Kommetjie (both harvested) and Scarborough North and South (both no-take) were used for spatial comparisons in 2017. In terms of wave action, the latter four sites rank as 'sheltered' to 'semi-exposed', whereas Wireless Island ranks as 'exposed' (as defined by Steffani & Branch 2003). For this reason, spatial comparisons excluded Wireless Island, and the temporal comparisons were made within each of the Wireless Point and Wireless Island sites. All sites fall within a single upwelling cell (Pfaff et al. 2011), thus eliminating upwelling as a variable.

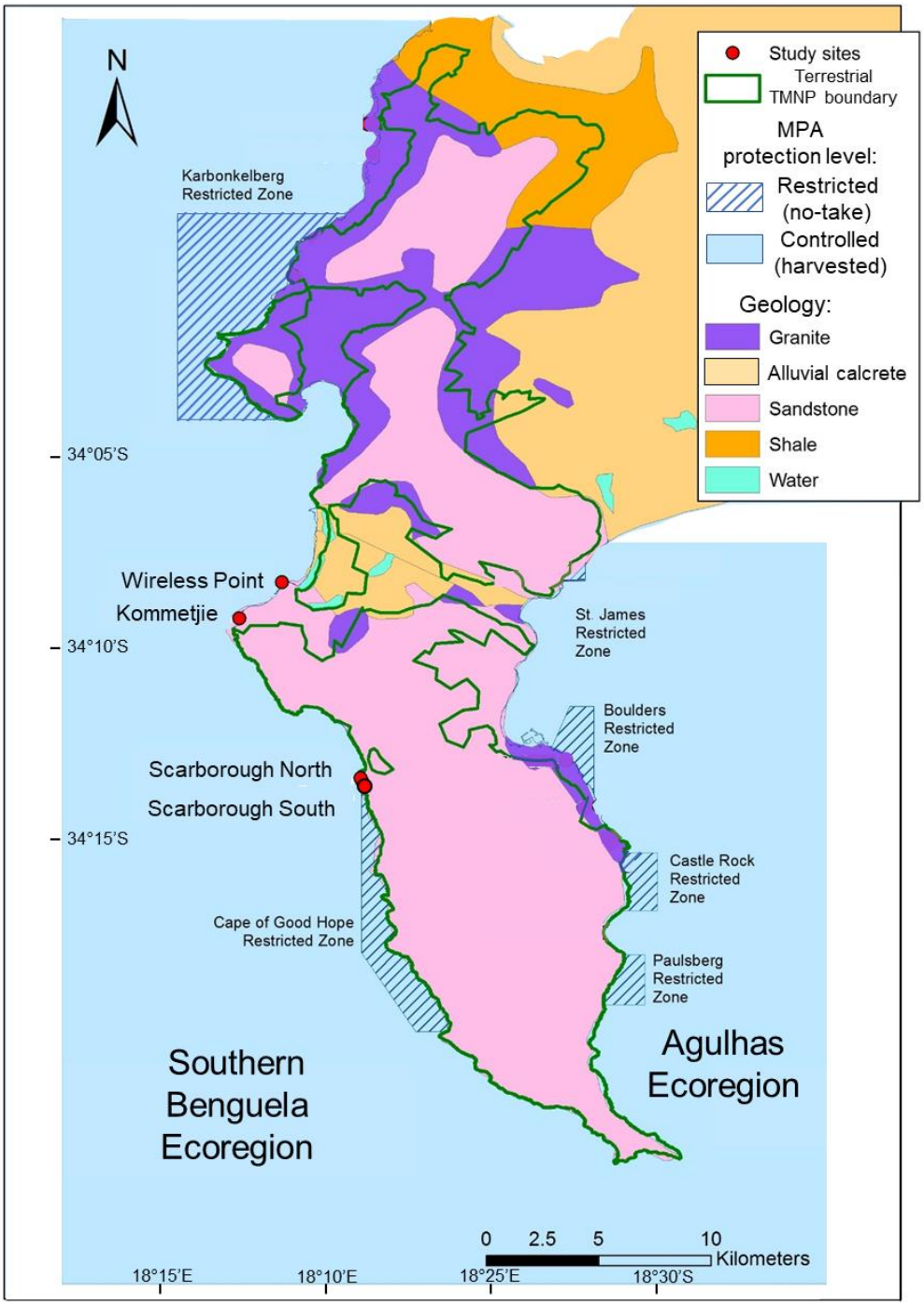



Figure 3.1. Map of the Table Mountain National Park Marine Protected Area (TMNP MPA) showing the study sites (red circles). Wireless Island and Point and Kommetjie are in a 'controlled' zone where harvesting is permissible, and Scarborough North and South in a 'restricted' no-take zone.

### *Study design for temporal and spatial comparisons*

I investigated the effects of harvesting and arrival of invasive alien mussels on rocky shores through temporal and spatial comparisons, following a combination of Before-After and Control-Impact designs (Underwood 2000, Smokorowski et al. 2017). The temporal component compared surveys I did in 2017 with historical data collected in 1970 (Branch 1975b; GM Branch, unpublished data) at Wireless Island and Wireless Point, before the invasion of *M. galloprovincialis* and before an increase in harvesting rates associated with expansion of the coastal human population near this site. Sampling protocols were exactly replicated between 1970 and 2017, and thus considered only the subsets of the community that were recorded in 1970. The spatial comparison focused on surveys in 2017 of two presently harvested and two unharvested sites (see above), which allowed an evaluation of the effects of harvesting on the community, using unharvested sites as controls.

### *Sampling methods for temporal and spatial comparisons*

For the temporal (Before-After) comparison of community structure, data were collected at Wireless Island and Wireless Point, repeating the methods used in 1970, as follows. On sloping platforms, five horizontal transects, each with five replicates, were sampled during spring tides at five heights on the shore (Fig. 3.2A), employing 50 x 50-cm quadrats that were spaced at equidistant intervals to span the range between the mean low and mean high water marks, in exactly the same locations and shore heights as those surveyed in 1970. Each quadrat was divided into 25 grid cells, each representing 4% cover, to facilitate accurate estimation of percentage cover. In each quadrat, all macro-invertebrate species and groups of algae (corticated algae, encrusting and ephemeral algae) were identified. The percentage cover of sessile organisms was estimated and the numbers of mobile fauna counted. The shell lengths of the commonly harvested *C. granatina* and *S. argenvillei* and the rarely harvested *S. granularis* found in the quadrats were measured using Vernier callipers. The historical data provided the best means of evaluating changes in density, size and community composition before and after the impacts of alien species and intensification of harvesting. However, no historical data existed for the protected sites, which prevented a complete Before-After-Control-Impact (BACI) design.

For the spatial comparison of community structure (Impact-Control component), separate surveys were conducted at the four sites in four intertidal zones (Fig. 3.2B) indicated by the following dominant species: low shore (*Scutellastra cochlear*); mid shore (*Pachymenia orbitosa*); high shore (*M. galloprovincialis* and *Scutellastra granularis*); and top shore (*Scutellastra granularis* and *Porphyra capensis*). Surveys covered the full tidal range (1.8 m), with 15 randomly placed replicate 50 x 50-cm quadrats sampled per zone, repeating procedures for the temporal sampling (see above), with the addition of measurements of shell lengths of *C. granatina*, *S. argenvillei* and *S. granularis* (n = 50 per zone in which they were present).

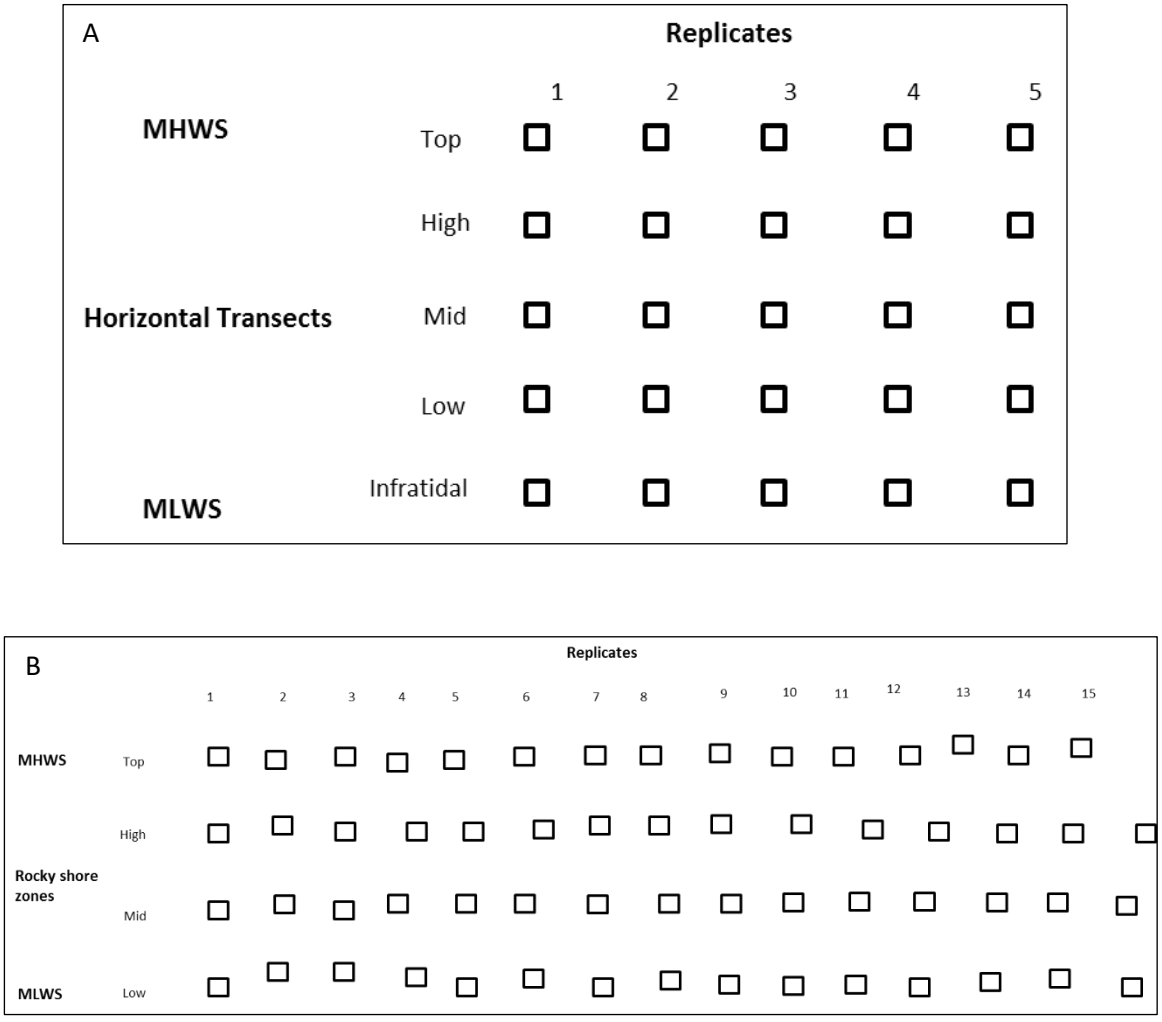



Figure 3.2. Sampling design for (A) temporal comparison at Wireless Island and Wireless Point (Before-After component, 1970 vs. 2017) and (B) spatial comparisons of four sites (Control-Impact component of sites in 2017). MHWS = mean high water springs and MLWS = mean low water springs. Squares indicate quadrats.

*Data analyses*

*(A) Temporal comparisons (Before-After component)*

To visualise differences in community composition between years (1970 vs. 2017) and among the five zones (i.e. the five horizontal transects), an unconstrained ordination based on Bayesian ordination analysis with two latent variables was fitted to the historical and current community data using the lvsplot in the R package BORAL (Hui 2015).

To test for statistical differences, I first performed a multivariate analysis of community composition, followed by univariate analyses of (a) two harvested species, namely *Cymbula granatina* (density and size data) and *Scutellastra argenvillei* (density data only, as no historical measures of sizes were available); and (b) one species that is not harvested, i.e., *S. granularis* (density and sizes). Finally, I compared the densities and sizes of *S. granularis* across zones, for 1970 and 2017, to explore possible changes in zonation in relation to the arrival of *M. galloprovincialis*.

A full factorial multivariate generalized linear model (manyglm, R package "mvabund", Wang et al. 2012, 2019) was used to assess differences in percentage cover (taxon-abundance) between years and among zones. Adherence to model assumptions was based on plotting the residuals against the fitted model (Wang et al. 2012). To probe differences and to identify taxa that contribute to differences, univariate tests were additionally run for each taxon, using the *p.uni*= "adjusted" argument.

To further examine the impacts of harvesting on the density and shell lengths of 'key species', the commonly harvested *C. granatina* and *S. argenvillei* and the rarely harvested *S. granularis* were compared between years (1970 vs 2017). A two-way ANOVA was applied after data were tested for normality and homogeneity of variance using Shapiro-Wilk's and Levene's tests, respectively. In cases where these assumptions were not met, data were square-root transformed. To evaluate the impacts of the invasion of the alien mussel *M. galloprovincialis* on the zonation patterns of *S. granularis*, two-way ANOVAs (with fixed factors years x zones) were applied to density and size data. The data were again tested for normality and homogeneity of variance, and were square root transformed to meet the model assumptions. In

cases where significant effects were found, Tukey multiple comparison post-hoc tests were used to explore the significance.

*(B) Spatial comparison (Control-Impact component)*

The Bayesian ordination and generalised linear model-based approaches used in the temporal analysis were not suitable for these analyses since the high number of species (dependent variables) prevented the models from converging. Multivariate percentage cover data for the four sites compared for spatial differences were thus visualised by an ordination using non-metric multidimensional scaling (MDS) performed in PRIMER (Plymouth Routines in Multivariate Ecological Research, Version 6.0).

To statistically investigate differences in community composition among sites of different protection levels, a two-way PERMANOVA with factor 'site' nested in 'protection level' was performed on the species-abundance data. The nested design was chosen to account for site-specific differences. Because the zones reflect different biotopes (i.e. different benthic communities), the analyses were done separately for each zone. Pairwise comparisons were done to test differences in community composition among sites. Prior to the analysis, data were standardised (by sample) and square-root transformed. To further explore the differences among sites and zones and to establish species or groups responsible for the observed differences, SIMPER (similarity percentage) analysis (with a cut off of 90%) was performed and only taxa contributing >2% are presented.

To evaluate the effect of harvesting on the densities and shell lengths of commonly harvested *C. granatina* and *S. argenvillei* and rarely harvested *S. granularis* among sites, a two-way ANOVA was performed on square-root transformed data to meet the assumptions of normality and homogeneity. In cases where significant differences were found, Tukey pairwise tests were used as post-hoc tests.

*(C) Species interactions*

To evaluate ecosystem effects of harvesting, I explored relationships among the abundances of limpets and each algal group (corticated, encrusting and ephemeral algae) by Pearson correlations. Given the dependency of P values on sample size, I included an estimation of the

effect size, as proposed by Cohen (1988, 1992); effect size was considered small for correlation coefficient (r) values around 0.1, medium for r ~ 0.3, and large for r ~ 0.5.

## Results

### *Temporal changes in community composition*

Rocky-shore community composition at both sites differed significantly between the years 1970 and 2017, but the magnitude of the differences varied depending on the intertidal zone, as reflected in a significant Year x Zone interaction (Table 3.1).

**Table 3.1**. Multivariate generalized linear model analysis of the community composition to test for differences between years and among intertidal zones, and their interaction. Asterisks indicate significant effects.

| **Wireless Island** | | | | | **Wireless Point** | | | |
|---|---|---|---|---|---|---|---|---|
| **Source** | **Res. Df** | **Df. Diff** | **Dev** | **Pr (>Dev)** | **Res. Df** | **Df. Diff** | **Dev** | **Pr (>Dev)** |
| Intercept | 48 | | | | 37 | | | |
| Year | 47 | 1 | 118.20 | 0.001* | 36 | 1 | 67.47 | 0.001* |
| Zone | 43 | 4 | 129.10 | 0.001* | 33 | 3 | 218.55 | 0.001* |
| Year × Zone | 39 | 4 | 121.90 | 0.001* | 30 | 3 | 47.38 | 0.003* |

At Wireless Island (Fig. 3.3A), two clusters were distinguishable: 1970, characterised by greater abundances of the limpets *S. barbara, C. oculus* and *C. granatina* and encrusting algae; and 2017, when corticated and ephemeral algae, the alien mussel *M. galloprovincialis* and, to a lesser extent, *S. granularis*, were more prevalent. At Wireless Point (Fig. 3.3B) the distinction between years was less clear-cut but still significant, with the 1970 cluster being driven by a greater abundance of encrusting algae, *C. granatina* and the ribbed mussel *Aulacomya atra*, and the 2017 cluster by more ephemeral algae, *S. granularis* and *C. oculus* (Fig. 3.3B).

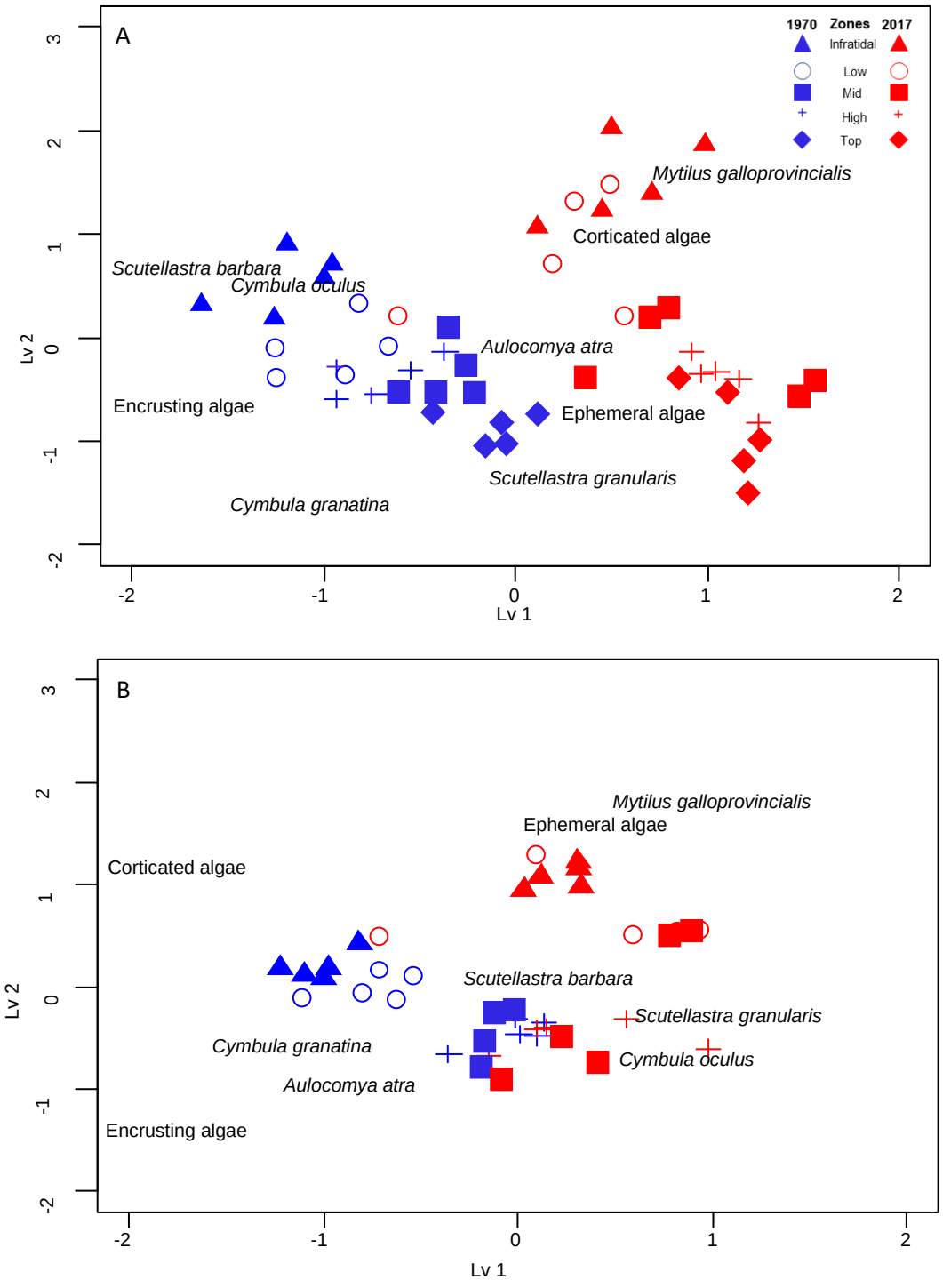



Figure 3.3. Unconstrained ordination with two latent variables (Lv1, Lv 2) based on taxon abundance data of quadrats (data points), showing differences between years (blue = 1970; red = 2017) and zones (different symbols – see key), at (A) Wireless Island and (B) Wireless Point. The naming of zones is shown in Figure 3.2A. The position of species and functional group names in the ordination portrays indicator species/groups characterising each of the respective years.

When further investigating each taxon, at Wireless Island significant differences among years (i.e. a significant main effect for Year) existed for *C. granatina*, which decreased from 1970 to 2017, and for corticated algae, *S. granularis* and *M. galloprovincialis*, which increased (Table 3.2). In fact, the alien mussel *M. galloprovincialis* was absent in 1970 but abundant in 2017. At Wireless Point, *A. atra*, *C. granatina* and *C. oculus* all declined significantly, whereas ephemeral algae increased (Table 3.2). As expected for intertidal communities, there were significant differences among zones in the abundances of the majority of groups (Table 3.2), i.e. for *C. granatina*, *S. barbara*, *C. oculus*, *M. galloprovincialis* and corticated algae at Wireless Island, and for *A. atra*, *S. granularis*, *C. granatina*, *C. oculus*, corticated and encrusting algae at Wireless Point.

At Wireless Island, a significant interaction between Year and Zone existed for *S. granularis* only (Table 3.2), and when further investigated, an interesting pattern emerged (see details in the following section). At Wireless Point, this interaction was also significant for (a) *A. atra* because it disappeared on the low shore and appeared on the high shore where it had not occurred in 1970; (b) *C. oculus* because its decline in 2017 was consistent but varied in magnitude among zones; and (c) ephemeral algae, which experienced increases in some but not all zones.

**Table 3.2**. Univariate tests for differences in abundance over time and among intertidal zones. P-values are adjusted for multiple testing using a step-down resampling algorithm (Wang et al. 2012). Goodness-of-fit of the models is indicated by the residual deviance (Dev), with lower values indicating better fit. Changes in the abundance over time are shown as increases (+), decreases (-) or no change (0). Blank cells = absence or scarcity that prevented analysis.

| | Wireless Island | | | Wireless Point | | |
|---|---|---|---|---|---|---|
| **Source** | **Dev** | **Pr (>Dev)** | **Change** | **Dev** | **Pr (>Dev)** | **Change** |
| *Mytilus galloprovincialis* | | | | | | |
| Year | 63.92 | <0.01 | + | | | |
| Zone | 18.55 | 0.02 | | | | |
| Year × Zone | 0.00 | 0.79 | | | | |
| *Aulacomya atra* | | | | | | |
| Year | 0.04 | 0.96 | 0 | 2.83 | 0.19 | |
| Zone | 3.23 | 0.33 | | 11.65 | 0.02 | |
| Year × Zone | 14.00 | 0.10 | | 10.65 | 0.04 | – |
| *Cymbula granatina* | | | | | | |
| Year | 9.52 | 0.01 | – | 32.01 | <0.01 | – |
| Zone | 16.62 | 0.02 | | 69.49 | <0.01 | |
| Year × Zone | 15.51 | 0.08 | | 8.97 | 0.06 | |
| *Cymbula oculus* | | | | | | |
| Year | 0.01 | 0.96 | 0 | 16.73 | <0.01 | |
| Zone | 28.98 | < 0.01 | | 12.43 | 0.02 | |
| Year × Zone | 7.15 | 0.35 | | 9.73 | 0.04 | - |
| *Scutellastra barbara* | | | | | | |
| Year | 0.22 | 0.89 | 0 | | | |
| Zone | 16.62 | 0.04 | | | | |
| Year × Zone | 8.26 | 0.27 | | | | |
| *Scutellastra granularis* | | | | | | |
| Year | 2.68 | 0.28 | 0 | 0.34 | 0.50 | 0 |
| Zone | 7.01 | 0.26 | | 58.61 | < 0.01 | |
| Year × Zone | 53.77 | <0.01 | | 2.25 | 0.77 | |
| Ephemeral algae | | | | | | |
| Year | 6.62 | 0.05 | + | 11.30 | 0.01 | |
| Zone | 6.41 | 0.26 | | 2.12 | 0.48 | |
| Year × Zone | 4.07 | 0.40 | | 14.86 | 0.02 | + |
| Corticated algae | | | | | | |
| Year | 33.56 | <0.01 | + | 1.42 | 0.24 | 0 |
| Zone | 23.66 | 0.01 | | 35.76 | <0.01 | |
| Year × Zone | 6.75 | 0.35 | | 0.33 | 0.77 | |
| Encrusting algae | | | | | | |
| Year | 1.60 | 0.38 | 0 | 4.21 | 0.10 | 0 |
| Zone | 10.50 | 0.10 | | 23.50 | <0.01 | |
| Year × Zone | 12.44 | 0.12 | | 1.237 | 0.77 | |

*Temporal comparisons of densities and sizes of key limpet species*

The density of *C. granatina* declined at both sites, but there was a significant interaction between year and site because the decline recorded at Wireless Point was much greater than at Wireless Island. Both sites had statistically comparable densities in 1970, but in 2017 Wireless Island had a significantly greater density than Wireless Point (Fig. 3.4A; Table 3.3). Density of the other commonly harvested limpet, *S. argenvillei* (present at Wireless Island only), also significantly declined between the years ($t = 5.28$, $df = 9$, $p < 0.001$; Fig. 3.4E). In contrast, densities of the rarely harvested limpet *S. granularis* were not significantly different between years at both sites, although a difference between the two sites became significant in 2017, with Wireless Island having greater densities than Wireless Point (Fig. 3.4C; Table 3.3).

Sizes (shell lengths) of *C. granatina* and *S. granularis* differed significantly between the years at Wireless Island, with the commonly harvested *C. granatina* decreasing in size ($t = 5.8327$, $df = 27$, $p < 0.001$), and the rarely harvested *S. granularis* increasing ($t = -4.769$, $df = 99$, $p < 0.001$) (Figs 3.4B and 3.4D). No historical data existed for sizes of *S. argenvillei*, preventing a temporal comparison of sizes for that species, and for *C. granatina* and *S. granularis*, historical size data were limited to Wireless Island.

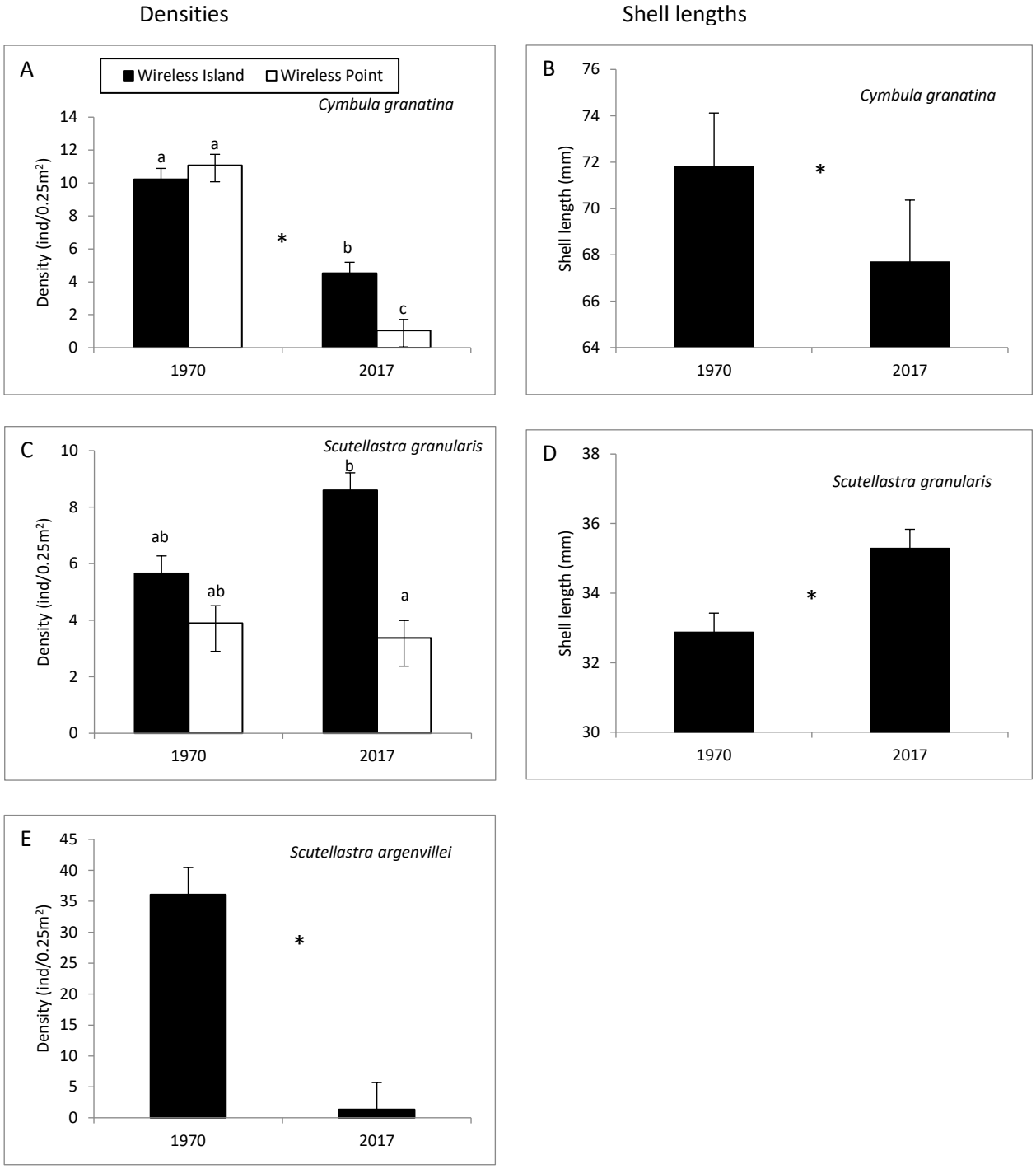



Figure 3.4. Mean (+1SE) densities (left) and sizes (right), showing differences between 1970 and 2017, for (A, B) *Cymbula granatina*, (C, D) *Scutellastra granularis* and (E) *S. argenvillei*. No historical length-data available for *S. argenvillei*; and it was absent from Wireless Point. Asterisks between years and different letters above error bars indicate significant differences ($P<0.05$).

**Table 3.3.** Two-way ANOVAs of the densities of *C. granatina* and *S. granularis* with factors Site and Time, and their interaction. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| *C. granatina* | | | | | |
| Site | 1 | 10.36 | 10.36 | 8.79 | <0.01* |
| Year | 1 | 64.76 | 64.76 | 54.94 | <0.01* |
| Site × Year | 1 | 11.70 | 11.70 | 9.92 | 0.01* |
| Residuals | 90 | 106.09 | 1.18 | | |
| *S. granularis* | | | | | |
| Site | 1 | 19.50 | 19.50 | 11.42 | <0.01* |
| Year | 1 | 0.12 | 0.12 | 0.07 | 0.80 |
| Site × Year | 1 | 0.33 | 0.33 | 0.19 | 0.66 |
| Residuals | 90 | 153.63 | 1.71 | | |

*Temporal changes in zonation of Scutellastra granularis*

At Wireless Island, there was a significant interaction of Year and Zone on the density of *S. granularis* indicating that changes in density of *S. granularis* over time varied among on the intertidal zones (Table 3.4). This reflects the fact that a gradual decrease in density from the low shore to the upper shore existed in 1970, whereas in 2017 densities progressively (and significantly) increased from the lower to the higher intertidal zones following the arrival of *M. galloprovincialis* (Fig. 3.5A, C). Effectively this reversed the previous zonation trend of consistently decreasing abundance with increasing shore height (Fig. 3.5A).

There also were significant effects of Year and Zone on the shell length (i.e. sizes) of *S. granularis* (Table 3.4), but they were confounded by a significant interaction, reflecting a reversal of patterns between years, similar to that observed for densities (Table 3.4; Fig. 3.5B, D). In 1970, large individuals were recorded in the top zone and small individuals in the infratidal zone, whereas in 2017 the opposite was found.

**Table 3.4**. Two-way ANOVA of the densities and sizes of *Scutellastra granularis* between years and among zones. Asterisks indicate significant effects.

| Source | Df | SS | MS | F-value | P-value |
|---|---|---|---|---|---|
| Density | | | | | |
| Year | 1 | 0.25 | 0.25 | 0.47 | 0.50 |
| Zone | 4 | 18.19 | 4.55 | 8.43 | <0.01* |
| Year × Zone | 4 | 54.16 | 13.54 | 25.11 | <0.01* |
| Residuals | 42 | 22.65 | 0.54 | | |
| Sizes | | | | | |
| Year | 1 | 23.75 | 23.75 | 56.45 | <0.01* |
| Zone | 4 | 114.85 | 28.71 | 68.25 | <0.01* |
| Year × zone | 4 | 40.87 | 10.22 | 24.29 | <0.01* |
| Residuals | 696 | 292.78 | 0.42 | | |

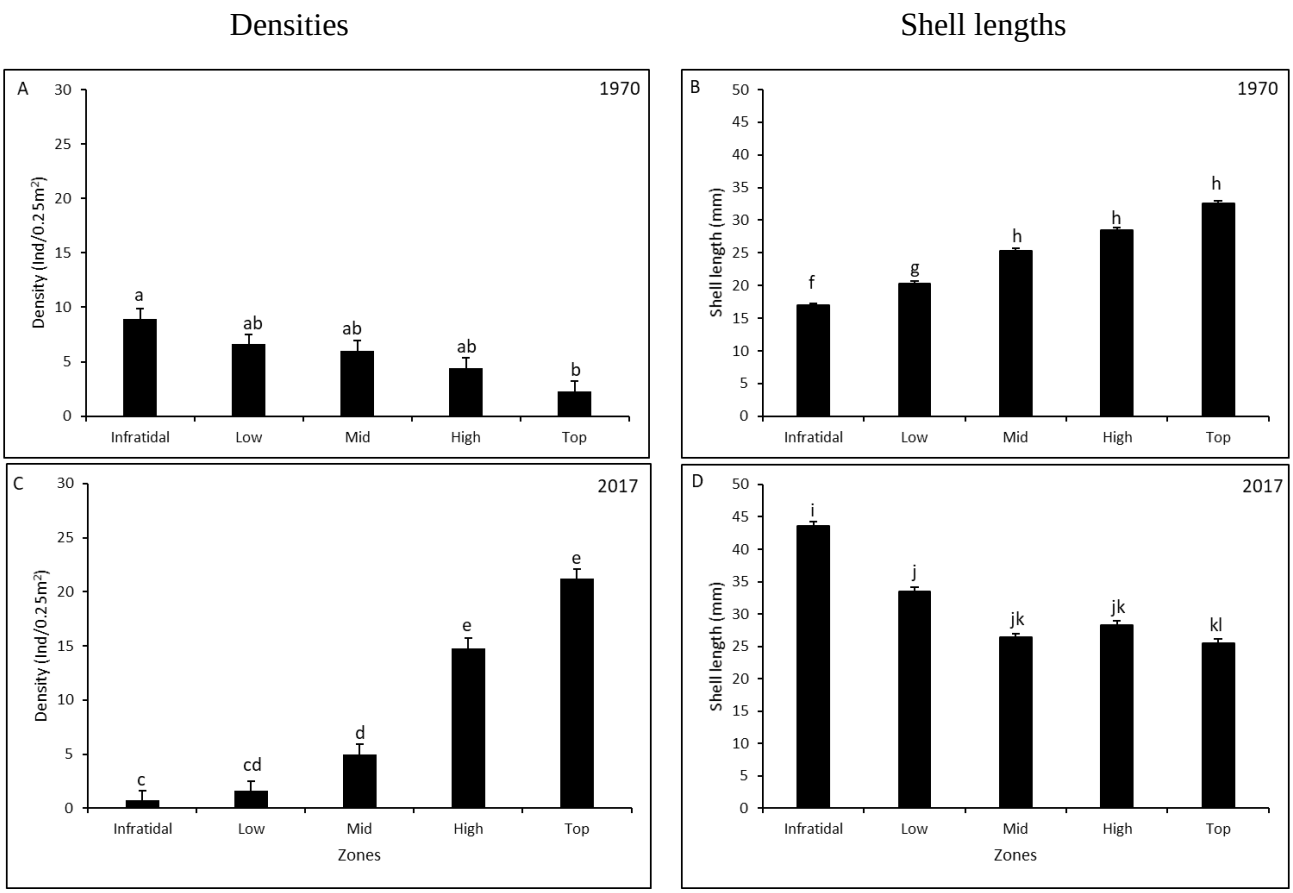



Figure 3.5. Comparisons of mean (+1SE) densities (A, C) and sizes (B, D) of *Scutellastra granularis* in different intertidal zones at Wireless Island in 1970, before the arrival of *Mytilus galloprovincialis* (A, B), and in 2017 after it has invaded (C, D). Lower case letters show Tukey HSD results with different letters indicating significant differences among zones and sites.

Community composition differed significantly between protection level and among sites (which were nested in Protection levels), in all intertidal zones (Table 3.5). In MDS plots (Fig. 33.6), the community compositions were separated from each other, with sites that are experiencing high harvesting pressure (Wireless Point and Kommetjie) positioned on one side of the plot and those that are protected (Scarborough North and Scarborough South) on the opposite side, except in the mid shore, where the two harvested sites were widely separated.

**Table 3.5.** Two-way nested PERMANOVA with factors protection level and site nested in protection level showing their effects on community composition in the four intertidal zones.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| **Low shore** | | | | | |
| Protection level | 1 | 53068.00 | 53068.00 | 35.25 | <0.01* |
| Site (Protection level) | 2 | 799.43 | 399.71 | 15758.00 | <0.01* |
| Residuals | 52 | 33735.00 | 648.76 | | |
| **Mid shore** | | | | | |
| Protection level | 1 | 19541.00 | 19541.00 | 17.09 | <0.01* |
| Site (Protection level) | 2 | 64301.00 | 21434.00 | 18.74 | <0.01* |
| Residuals | 58 | 66336.00 | 1143.70 | | |
| **High shore** | | | | | |
| Protection level | 1 | 29204.00 | 29204.00 | 32.71 | <0.01* |
| Site (Protection level) | 2 | 79896.00 | 26632.00 | 29.83 | <0.01* |
| Residuals | 50 | 44636.00 | 892.72 | | |
| **Top shore** | | | | | |
| Protection level | 1 | 31433.00 | 31433.00 | 23.30 | <0.01* |
| Site (Protection level) | 2 | 70560.00 | 23520.00 | 36.25 | <0.01* |
| Residuals | 52 | 33735.00 | 648.76 | | |

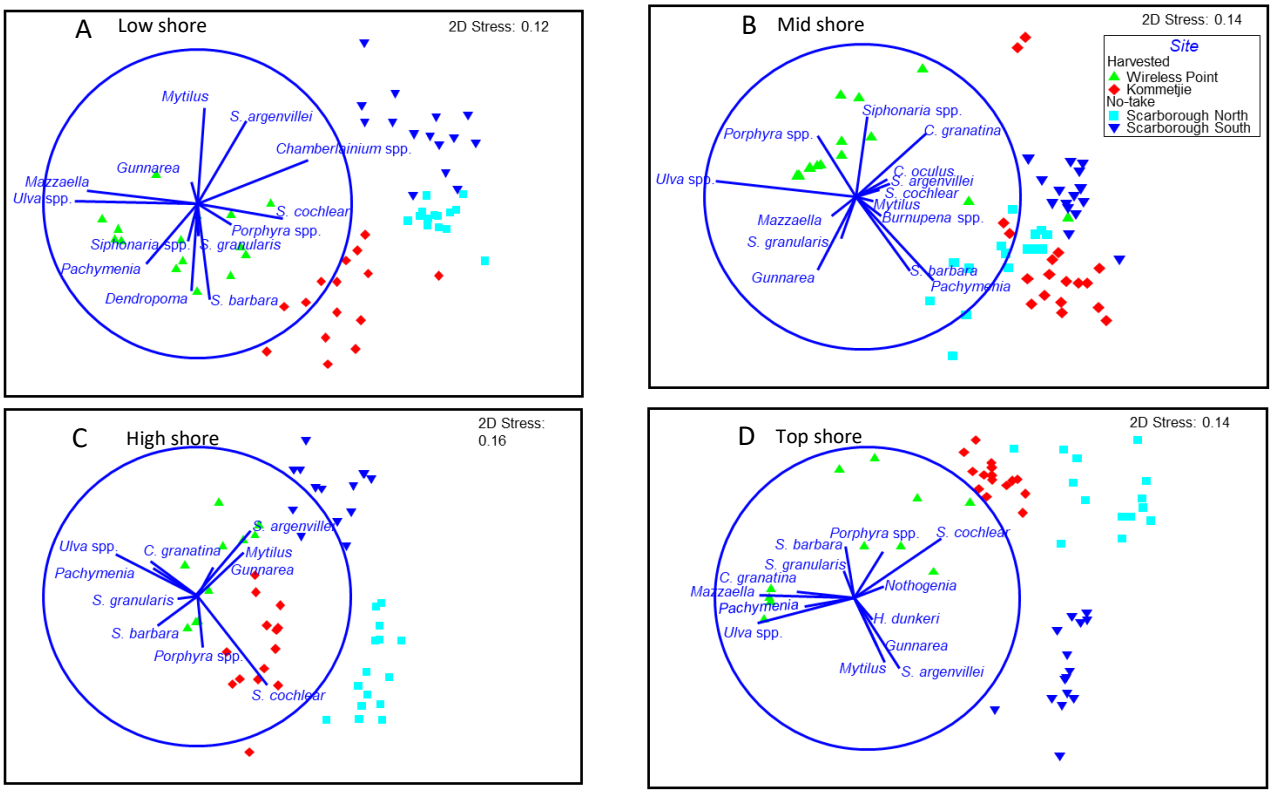



Figure 3.6. Multidimensional scaling (MDS) of species abundance in the four zones: (A) low shore, (B) mid shore, (C) high shore and (D) top shore, reflecting differences in community composition among sites: Kommetjie and Wireless Point are harvested, whereas Scarborough North and Scarborough South are protected. Diagnostic species in the different sites are also presented in blue font as vectors based on correlations.

Pairwise comparisons showed high dissimilarities in community composition among sites and protection levels (Table. 3.6). Fifteen species were responsible for the major differences (Fig. 3.6 blue vectors, Fig.3.7 black dots). Macroalgae (*Mazzella capensis*, *Pachymenia orbitosa*, *Ulva* spp. and sometimes *Porphyra* spp.) prevailed at the harvested sites of Wireless Point and Kommetjie. In contrast, the two protected Scarborough sites displayed greater cover of *Mytilus galloprovincialis*, especially in the top and high shores, and most obviously at Scarborough South. A dense bed of *C. granatina* in the midshore discriminated the protected Scarborough sites from those of the harvested sites at Wireless Point and Kommetjie, and it was also extremely abundant in the high shore at Scarborough North. Additionally, two limpets, *S. cochlear* and *S. argenvillei*, together with associated encrusting algae *Chamberlainium* spp., prevailed in the low shore at the protected Scarborough sites while being less common at

Wireless Point and Kommetjie. *Scutellastra granularis* emerged as dominant in this zone at all four shores.

**Table 3.6.** The Bray-Curtis dissimilarities in community composition among sites in the four intertidal zones based on pairwise comparisons.

| | Scarborough North | Scarborough South | Wireless Point |
|---|---|---|---|
| Low shore | | | |
| Scarborough South | 56.06 | | |
| Wireless Point | 92.08 | 95.38 | |
| Kommetjie | 62.06 | 74.22 | 72.87 |
| Mid shore | | | |
| Scarborough South | 57.83 | | |
| Wireless Point | 84.38 | 87.22 | |
| Kommetjie | 54.31 | 55.97 | 82.51 |
| High shore | | | |
| Scarborough South | 92.75 | | |
| Wireless Point | 88.26 | 94.54 | |
| Kommetjie | 54.31 | 55.97 | 58.82 |
| Top shore | | | |
| Scarborough South | 92.79 | | |
| Wireless Point | 93.14 | 95.18 | |
| Kommetjie | 48.60 | 68.83 | 59.15 |

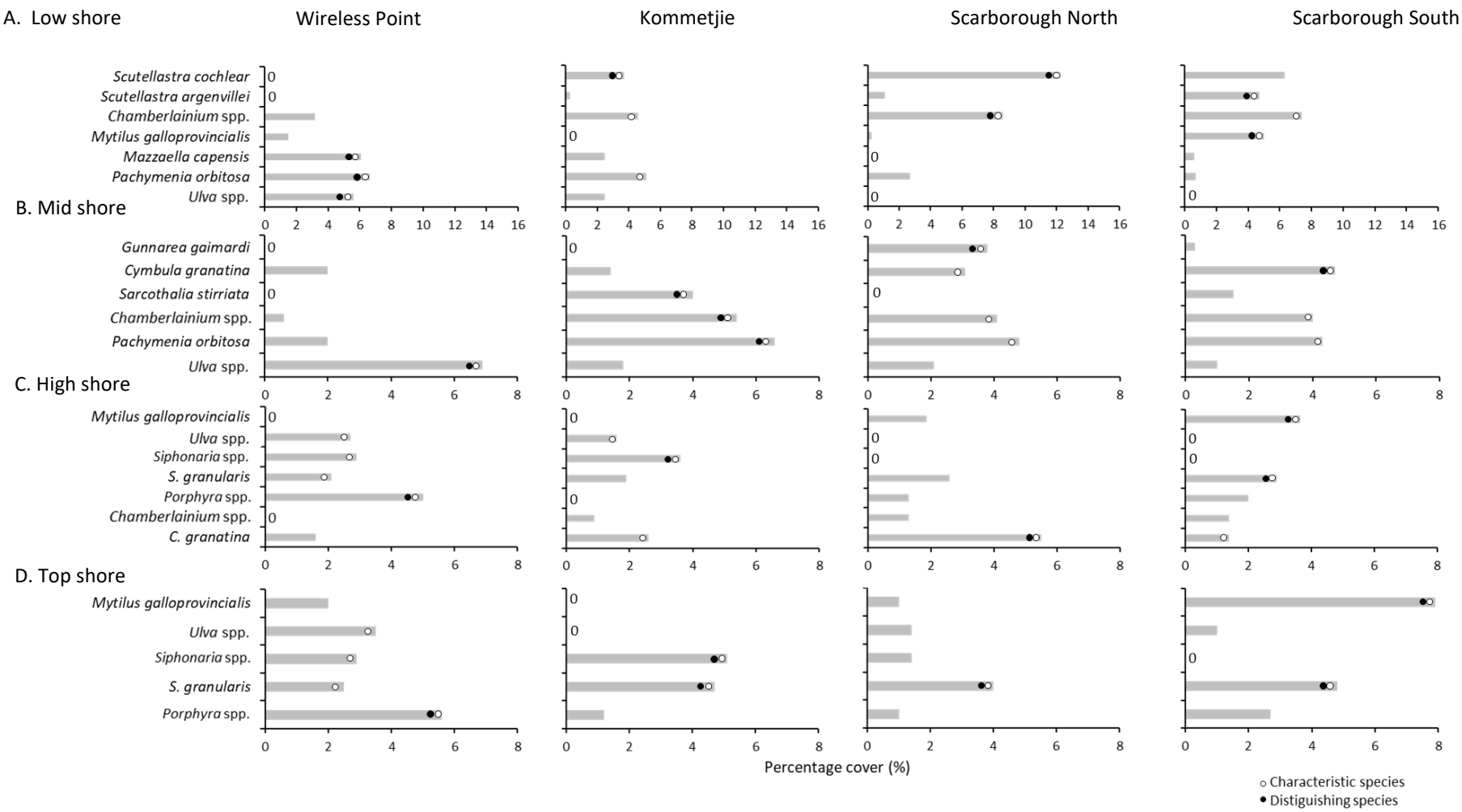



Figure 3.7. Percentage cover (square-root transformed) of species responsible for the similarities within sites in (A) low, (B) mid, (C) high and (D) top shores, and the dissimilarities between Wireless Point, Kommetjie, Scarborough South and Scarborough North. White dots identify species characteristic of each site; black dots identify species distinguishing between sites (based on SIMPER analysis) and are placed in the site with the greater or greatest abundance; 0 = absence.

*Spatial differences in density and shell length of key species*

Densities of the limpet *C. granatina* were less at the harvested areas than in the no-take areas, with the density at Scarborough South being intermediate and not differing significantly from those at the other sites (Table 3.7, and post-hoc letters shown in Fig. 3.8A). Shell lengths of *C. granatina* also showed significant effects of protection level and sites (Table 3.8; Fig. 3.8B), being smallest at Wireless Point, largest at Scarborough South (the site that lies farthest inside the sanctuary area), and intermediate at Kommetjie and Scarborough North.

*Scutellastra argenvillei* attained greater average densities inside the no-take area, with by far the highest densities found at Scarborough South, while few individuals occurred at the other sites (Table 3.7; Fig. 3.8C). The shell lengths of this species were unambiguously larger inside the no-take Scarborough sites than in the harvested Wireless Point and Kommetjie sites (Table 3.8; Fig. 3.8D).

Densities of the rarely harvested *S. granularis* differed significantly among sites, but not between protection levels (Table 3.7; Fig 3.8E). While density was low at Wireless Point, it did not differ statistically from that of Scarborough North, and density at Scarborough South was not statistically different from that at Kommetjie (Fig. 3.8E). Shell lengths were also not affected by protection levels (Table 3.8), with Scarborough North and South being intermediate between the low values at Kommetjie and the high values at Wireless Point (Table 3.8; Fig. 3.8F). Density thus appeared to be negatively related to mean size, although it was not possible to test this statistically with a sample size of only four sites.

**Table 3.7.** Results of two-way nested ANOVAs of the densities of *C. granatina*, *S. argenvillei* and *S. granularis* with factors protection level and site nested in protection level. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| *C. granatina* | | | | | |
| Protection level | 1 | 31.80 | 31.84 | 9.39 | <0.01* |
| Site (Protection level) | 2 | 39.90 | 13.30 | 3.92 | <0.01* |
| Residuals | 172 | 583.01 | 3.39 | | |
| *S. argenvillei* | | | | | |
| Protection level | 1 | 75.11 | 75.11 | 54.03 | <0.01* |
| Site (Protection level) | 2 | 90.85 | 45.42 | 32.67 | <0.01* |
| Residuals | 56 | 77.86 | 1.39 | | |
| *S. granularis* | | | | | |
| Protection level | 1 | 12.80 | 12.80 | 3.86 | 0.05 |
| Site (Protection level) | 2 | 23.40 | 11.71 | 3.53 | 0.03* |
| Residuals | 230 | 763.20 | 3.32 | | |

**Table 3.8.** Results of two-way nested ANOVAs of the shell lengths of *C. granatina*, *S. argenvillei* and *S. granularis* with factors protection level and site nested in protection level. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| *C. granatina* | | | | | |
| Protection level | 1 | 41.50 | 41.50 | 20.13 | <0.01* |
| Site (Protection level) | 2 | 23.60 | 11.80 | 5.72 | <0.01* |
| Residuals | 209 | 430.90 | 2.06 | | |
| *S. argenvillei* | | | | | |
| Protection level | 1 | 79.76 | 79.76 | 59.57 | <0.01* |
| Site (Protection level) | 2 | 61.45 | 30.73 | 22.95 | <0.01* |
| Residuals | 218 | 291.87 | 1.34 | | |
| *S. granularis* | | | | | |
| Protection level | 1 | 3.10 | 3.13 | 2.58 | 0.11 |
| Site (Protection level) | 2 | 132.40 | 66.21 | 54.45 | <0.01* |
| Residuals | 291 | 353.90 | 1.22 | | |

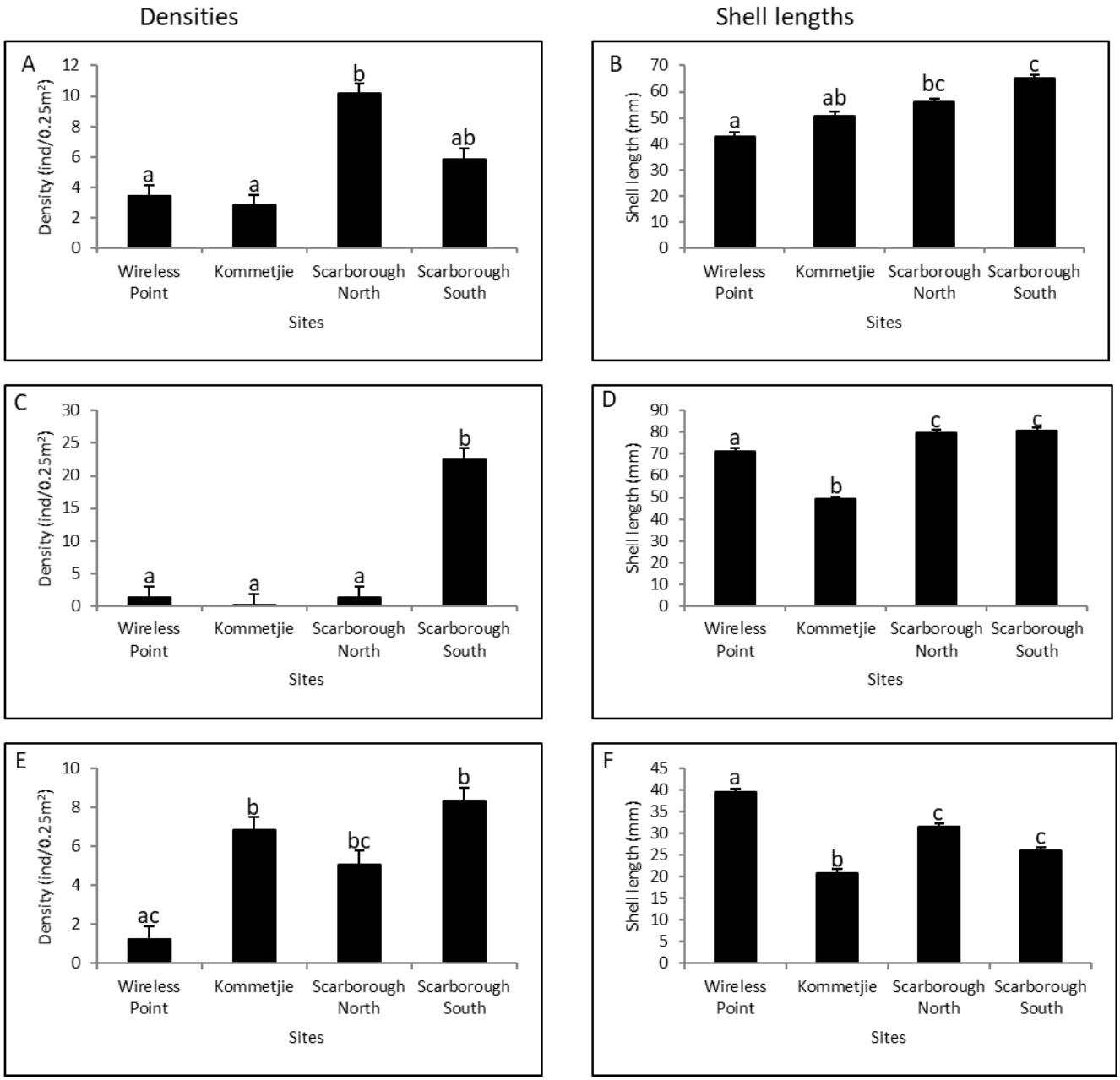



Figure 3.8. Mean (+1SE) densities (left panels) and shell lengths (right panels) of the limpets (A-B) *Cymbula granatina*, (C-D) *Scutellastra argenvillei* and (E-F) *Scutellastra granularis* at the four study sites. Different letters indicate significant differences according to posthoc tests and refer to comparisons within each panel.

*Correlations between limpet density and algal cover*

A number of trends emerged from correlations between limpet densities and percentage cover of different algal groups, despite a fair amount of variance in the data. Effect sizes were medium for ephemeral ($r = -0.30$) and corticated ($r = +0.39$) algae and large for encrusting algae ($r = +0.54$) (Fig. 3.9). I am thus confident that these relationships are real and not just a result of large sample sizes. The percentage cover of ephemeral algae declined with an increase in limpet abundance and reached a peak in areas with <3% cover of limpets (Fig. 3.9A), whereas the percentage cover of corticated algae was better explained by a quadratic relationship since it first rose with limpet density, to a peak at around 27% cover of limpets and then fell at higher levels of abundance (Fig. 3.9B). Encrusting algae, on the other hand, displayed a linear positive relationship with limpet densities (Fig. 3.9C). All these patterns must be treated with caution because of the magnitude of the variance and because of violations of homogeneity of residuals, so I used these results to interpret trends in the data and not for exact predictions.

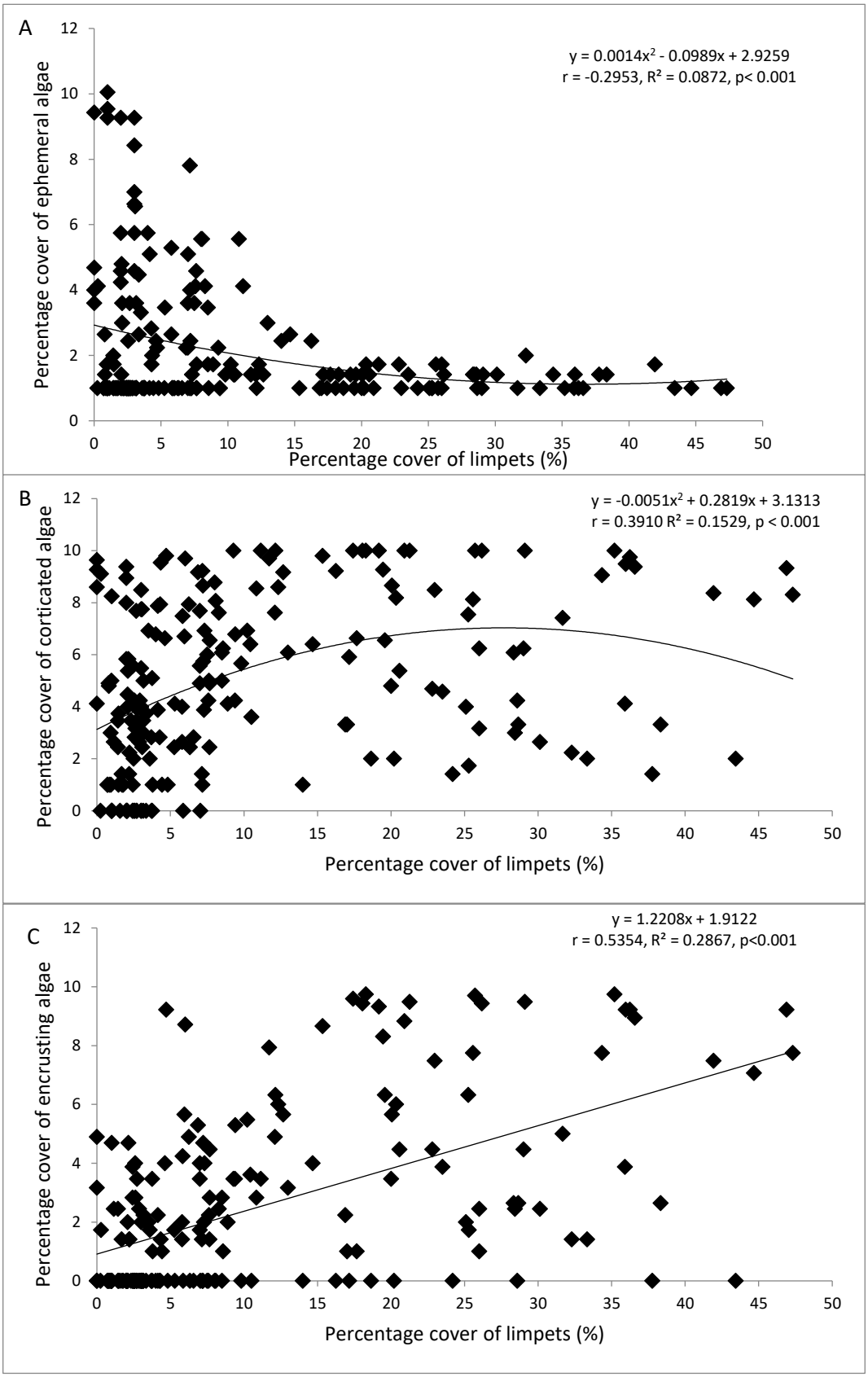



Figure 3.9. Relationships between the density of limpets and (A) ephemeral algae, (B) corticated algae and (C) encrusting algae and supporting statistics from regression analyses (for x+1 values in case of (A)).

## Discussion

This study assessed the impacts of harvesting and the establishment of an invasive species on rocky shore biodiversity of the Table Mountain National Park MPA (TMNP MPA) through a combination of temporal and spatial comparisons. The temporal comparison revealed major changes in the densities and shell lengths of limpets as well as in overall community composition at the two sites that were compared between 1970 and 2017, namely Wireless Island and Wireless Point. There were marked declines in densities of the two most-commonly harvested limpets, *Cymbula granatina* and *Scutellastra argenvillei*. In contrast, densities of the rarely harvested *Scutellastra granularis* remained the same. Other differences included the reversed ontogenetic zonation patterns of *S. granularis*, which were associated with the arrival of the alien mussel *M. galloprovincialis* and the proliferation of macroalgae associated with a decline in limpets.

Spatial comparisons made in 2017 between the two protected sites (Scarborough North and South) and the two harvested sites (Wireless Point and Kommetjie) revealed that community composition markedly differed between protection levels and among the four sites. Densities and sizes of the two commonly harvested limpets, *Cymbula granatina* and *Scutellastra argenvillei*, were greater at the protected sites although the magnitude of this effect was site-dependent. Values for the rarely harvested *S. granularis* differed among sites, but not in a manner related to the level of protection. Macroalgae were more abundant at harvested than protected sites.

Differences among sites are not unexpected, given that significant differences in community composition have frequently been noted among rocky shores, even when they are separated by short distance of 10s of km (Fraschetti et al. 2005b, Valdivia et al. 2011, La Valle et al. 2020). In some cases, such differences have been attributed to variations in benthic recruitment (Watson & Barnes 2004), which in turn have been linked to differences in factors such as wave action and upwelling (Pfaff et al. 2011, Hoffmann et al. 2012). But in my study, all the sites I examined fell within a single upwelling cell (Pfaff et al. 2011) and I standardised wave action by selecting shores that lay within a limited range of wave action conditions. The contrasts I recorded in space and in time are thus more obviously linked to differences and changes in harvesting intensity, and the arrival and spread of an alien species.

*Temporal changes in community composition*

Relatively few comparisons of rocky shores have been made over long periods of time. Sadchatheeswaran et al. (2015) recorded the transformation of island rocky-shore communities over the period 1980 to 2012 caused by successive arrivals of alien species. In Florida, Smith et al. (2007) detected considerable changes in 1999 from historical baselines that were established in 1947, and invoked pollution and harvesting to explain reductions or disappearances of some species, and suggested that changes in the abundance of grazers, coupled with eutrophication accounted for an upshore shift in algae. Decadal changes in the algal composition of Hawaiian Islands have been ascribed to increases in sea temperature and nutrient inputs (La Valle et al. 2020). Using data collected in California 1931-1933, Sagarin et al. (1999) documented that species composition in 1993-1996 had changed in a manner consistent with the predicted effects of oceanic warming, with a large majority of southern (warm-water) species increasing in abundance, whereas most northern (cooler-water) species declined. In contrast, Poloczanska et al. (2011) could find no evidence of latitudinal changes in rocky-shore communities in eastern Australia over a 60-year period, despite evidence of a rise in sea temperature of around 1.5°C. Both the magnitudes and the causes of changes are thus diverse.

My data reveal substantial changes in both community composition and the abundances and sizes of species over the period 1970 to 2017, which can have two potential explanations. The first is the arrival and establishment of the alien Mediterranean mussel *M. galloprovincialis*, and the second is the increase in harvesting over time, which led to a decrease in the density of limpets, particularly *C. granatina* (which was the species harvested most intensely), and consequent increases in abundances of corticated and ephemeral algae. *Mytilus galloprovincialis* is a major contributor to changes in community composition worldwide, and has been shown to drive shifts in rocky-shore community structure in South Africa in a number of ways (Robinson et al. 2007, Sadchatheeswaran et al. 2015). Due to its high tolerance to desiccation, high growth rate and fecundity, *M. galloprovincialis* outcompetes indigenous species, monopolises mid to high zones and creates a complex habitat that ameliorates harsh conditions and supports a rich fauna in its interstitial spaces (Griffiths et al. 1992, Ruiz Sebastián et al. 2002, Steffani & Branch 2003, Robinson et al. 2007, Sadchatheeswaran et al. 2015). The secondary habitat formed by this mussel led to increases in the density of *S.*

*granularis* in the top and high zones and declines in the infratidal and low zones where they were previously most abundant. Following the arrival of *M. galloprovincialis*, increases in the abundance of *S. granularis* juveniles in mussel beds and diminishment of adults on the shrinking primary space have previously been reported on the west coast of South Africa (Griffiths et al. 1992, Robinson et al. 2007, Branch et al. 2008, 2010, Sadchatheeswaran et al. 2015).

A second contributor to the difference in community composition over time was an intensification of harvesting, which was non-existent or minimal at the surveyed sites in 1970. Associated with this, there was a reduction in targeted limpet species and increases in percentage cover of various macroalgal groups, attributable to reduced grazing pressure on algae (Lodge 1948, Hockey & Bosman 1986, Dye & White 1991, Lindberg et al. 1998, Dye 1995, 1998, Lasiak & Field 1995, Lasiak 1998, Martins et al. 2008, 2010a, Portugal et al. 2017). The types of algae that came to predominate differed among sites, with ephemeral species increasing at Wireless Point and corticated species at Wireless Island. This may reflect differences in the abundances of limpets, as the main harvested species, *C. granatina*, was depleted to a greater extent at the more easily accessible Wireless Point. Density of limpets is known to influence the types and amounts of algae that develop (Dye 1993, 1995, Micheli et al. 2005, Maneveldt et al. 2009, Babcock et al. 2010, Martins et al. 2010a, Aguilera & Navarrete 2012, Deepananda & Macusi 2013, Almeida et al. 2016, Riera et al. 2016). At Wireless Point, where only few individuals of *C. granatina* remain on the low shore, ephemeral algae have taken over the intertidal rocky shores. The decline in *C. granatina*, which used to dominate the community composition at both Wireless Island and Wireless Point, is not likely to be due to the arrival of *M. galloprovincialis*, as the mussel inhabits mid to top zones and prevails on exposed shores (Steffani & Branch 2003), whereas this limpet mainly occupies the low shore and is most abundant on sheltered to semi-exposed shores (Bustamante et al. 1995a). Thus, the decline in *C. granatina* can more likely be ascribed to increases in the human population adjacent to the rocky shore and associated intensification of harvesting (Eekhout et al. 1992, Emanuel et al. 1992, Griffiths & Branch 1997), as will be discussed in detail below.

*Temporal comparisons of densities of key species*

The temporal comparisons demonstrated that densities of commonly harvested limpet species have declined substantially over the years. In the past, populations of *C. granatina* and *S. argenvillei* formed dense beds with densities of respectively 70-288/$m^2$ (equivalent to 17.5-37/0.25$m^2$) and 162-216/$m^2$ (equivalent to 54/0.25$m^2$). Previous densities at the sites I examined equated well with those at other unharvested sites (Eekhout et al. 1992, Bustamante et al. 1995a, Steffani & Branch 2003, 2005). Currently, the populations of *C. granatina* and *S. argenvillei* at Wireless Point and Wireless Island have declined by 56% and 97% respectively. These levels of decline far exceed those reported elsewhere for experimental thinning of *C. granatina* and *S. argenvillei*, which were reduced respectively down to 33.4% and 25% of their original densities of individuals ≥60 mm and ≥75mm (Eekhout et al. 1992). Even at those levels of depletion, however, ecosystem effects were detectable. The levels of depletion I recorded are comparable to those reported for other limpet species considered to be experiencing high harvesting pressure, such as 50% for *S. longicosta* (Lasiak 1991b) and 75% for *C. oculus* (Branch & Odendaal 2003) on the east coast of South Africa. In contrast, I found that the rarely harvested *S. granularis* displayed an average 25% (non-significant) increase in density over the years. The lack of any significant change in density of rarely harvested *S. granularis* while commonly harvested species were declining supports the idea that harvesting was the main cause of their decline. Intensification of harvesting of the two species is likely attributable to a rise in the density of human populations, in the vicinity of Cape Town in general (Griffiths & Branch 1997, Reimers et al. 2014, Pfaff et al. 2019) and near the Wireless study sites in particular, where the steadily growing low-income settlement of Masiphumelele was established in the 1980s.

Comparing the two harvested sites, significantly greater densities of *C. granatina* at Wireless Island, compared to Wireless Point, are probably a reflection of the relatively low harvesting pressure at Wireless Island because it is detached from the mainland and less accessible. Inaccessibility of rocky shores is well known as a factor that reduces harvesting pressure on intertidal gastropods (Addessi 1994, Benedetti-Cecchi et al. 2003b, Ceccherelli et al. 2005, Rivera-Ingraham et al. 2011, Sousa et al. 2019). In line with this, greater densities of *Phorcus turbinatus*, *Patella ferruginea* and *Patella ulyssiponensis* have been reported on inaccessible islands compared to accessible mainland sites in Italy (Ceccherelli et al. 2011, Coppa et al.

2012, 2015), and inaccessibility of sites has also been shown to be associated with greater densities of *Haliotis spadicea* and *Scutellastra longicosta* in South Africa (Lasiak 1991a, 1992), the mussel *M. galloprovincialis* in Portugal (Rius & Cabral 2004, Veiga et al. 2020), as well as the alga *Durvillaea antarctica* in Chile (Bustamante & Castilla 1990). However, higher density of *S. granularis* at Wireless Island than at Wireless Point may indicate that the species is indirectly benefitting from the greater exposure to wave action there, as the alien mussel *M. galloprovincialis* is known to benefit from wave action (Bustamante & Branch 1996b), and provides secondary habitat that boosts the numbers of juveniles of *S. granularis* (Griffiths et al. 1992, Robinson et al. 2007, Branch et al. 2008, 2010, Sadchatheeswaran et al. 2015).

### *Temporal comparisons of shell lengths of key species*

The decline in shell lengths of the commonly harvested *C. granatina* over time is consistent with effects of harvesting because large individuals are targeted as food (Branch 1975a, Roy et al. 2003, Riera et al. 2016, Bednar & Trulio 2017), a phenonemon that has been recorded even from prehistoric times (Rogers & Weisler 2019). Declines in shell lengths of harvested species, e.g. *Loggia gigantea* (Roy et al. 2003), *Patella candei crenata*, *Patella aspera* (Riera et al. 2016) and *Tegula funebralis* (Bednar & Trulio 2017), are common worldwide, especially in areas adjacent to residential developments that are frequently visited by shellfish gatherers (Riera et al. 2016). However, other factors such as competition and resultant declines of food sources can also reduce average sizes of limpets (Branch 1975b, 1976). Even gastropods that are not harvested, such as *Nucella lapillus* and *Siphonaria lessonii*, display reduced shell length over time if food availability decreases due to competition (Moreno et al. 1984, Wilson-Brodie et al. 2017). However, competition is unlikely to explain the reduction in size of *C. granatina* since its size reduced in parallel with a reduction in density, and at least in its adult stage it is in any case a 'trapper' that relies on trapping drift algae and is therefore relatively independent of local epilithic algal supplies (Bustamante et al. 1995a). Moreover, *S. granularis*, which is rarely harvested, increased in shell length over time in the same area. When harvesting was prevented in an MPA in Chile, the shell lengths of the two commonly harvested limpets *Fissurella picta* and *L. gigantea* increased increased over time despite their density rising (Moreno et al. 1984). These observations are strong supporting evidence that harvesting, rather than competition, caused the declines I recorded in sizes of harvested species (Lucas & Smith 2016). These facts, together with the observation that shell length of *S. granularis* increased

over time strengthen the argument that harvesting was the cause of decline in shell lengths of *C. granatina*.

### *Temporal changes in the zonation of Scutellastra granularis*

My study is the first to report the effect of the alien *M. galloprovincialis* on the zonation patterns of *S. granularis*. Invasion by this mussel has shifted the centre of recruitment of *S. granularis* from the infratidal and bottom zones to the mid and high shore. Prior to the arrival of *M. galloprovincialis*, densities of *S. granularis* decreased upshore and its average size increased upshore – to the extent that Branch (1975b) classed it as one of a group of 'migratory' species that settle low on the shore and then shift progressively to higher levels. The arrival of *M. galloprovincialis* has seen not only an increase in densities of this limpet at Wireless Island, but a concentration of its recruits among beds of *M. galloprovincialis* and a downward movement of adults as they move from the mussel beds to vacant space below the beds. These findings are in agreement with results of Griffiths et al. (1992) and Branch et al. (2008, 2010) who reported low density of *S. granularis* in areas where *M. galloprovincialis* is absent or scarce along the west coast. The low density of *S. granularis* in the infratidal zone further supports earlier findings on the influence of *M. galloprovincialis* on the density of *S. granularis*, which have been reported for various sites along the west coast of South Africa (Griffiths et al. 1992, Robinson et al. 2007, Branch et al. 2008, 2010, Sadchatheeswaran et al. 2015). The phenomenon of facilitation of gastropods by mussels is not unique to the sites where I worked, For example, in Chile the limpet *Siphonaria lessoni* and the whelk *Nacella magellanica* attain higher densities in beds of the mussel *Perumytilus purpuratus* than on bare rock (Bertness et al. 2006).

Prior to the arrival of *M. galloprovincialis*, the zonation of *S. granularis* reflected a pattern typical of many 'up shore' species, such as *Lottia digitalis*, *Collisella subrugosa*, *Helcion concolor*, or *Siphonaria guamensis*, for which recruitment occurs low on the shore and individuals migrate upshore as they become larger (Branch 1975a, 1975b, 1976, Hobday 1995, Tanaka et al. 2002, Chim & Tan 2009). However, the invasion by *M. galloprovincialis* has altered the size zonation patterns of *S. granularis* and recruits and juveniles are now found predominantly in the mid to upper zones and adults in the infratidal zone. This reflects the fact

that *M. galloprovincialis* has ameliorated the previously harsh conditions on the high shore, which usually limit settlement of recruits to the low shore, so that *M. galloprovincialis* promotes recruits and juvenile survival (Branch 1975a, 1976, Wootton 1993, Hobday 1995, Robinson et al. 2007, Branch et al. 2010, Sadchatheeswaran et al. 2015). Similar interactions have been observed on the south coast of South Africa, between *S. granularis* juveniles and barnacles, where the presence of barnacles on the high shore improves conditions, leading to greater recruitment of *S. granularis* there (Branch 1976). Conversely, Ellrich et al. (2020) have recorded how limpets reduce barnacle recruitment. The presence of large-sized *S. granularis* in the infratidal zone indicates a downward migration of individuals as they grow into the zone where there are few individuals of *M. galloprovincialis*. Previous studies have shown that adult *S. granularis* inhabit patches of bare rock that are devoid of *M. galloprovincialis* and small ones predominate in mussel beds (Griffiths et al. 1992). The downwards movement might avoid competition for space in the high shore where primary space suitable for adult *S. granularis* is limited, and algal food supplies reduced. Removal of *M. galloprovincialis* results in an increase in the density of adult *S. granularis* on the primary space that becomes available (Branch et al. 2010). Similarly, Tanaka et al. (2002) reported a positive correlation between the amount of bare rock and the sizes of the limpet *Collisella subrugosa* on the high shores of Brazil. This demonstrates the need for adequate primary space by adult limpets, and limitations on space availability on the top zone due to monopolisation by *M. galloprovincialis* have forced adults to reverse the previous upshore migratory behaviour described by Branch (1975b).

### *Spatial differences in community composition*

Differences in the community composition between rocky-shore sites experiencing high harvesting pressure and those protected from harvesting have been reported many times in South Africa and worldwide (Lasiak & Field 1995, Lasiak 1998, 1999, Deepananda & Macusi 2012, Fraschetti et al. 2012, Jimenez et al. 2015, Portugal et al. 2017). Experimental removal of limpets has often demonstrated this (Lodge 1948, Maneveldt et al. 2009). Very often, removals of limpets and mussels from the rocky shores lead to increases in the cover of macroalgae. The increase in the macroalgal cover might in turn inhibit the settlement and recruitment of species that require primary substrate or a cover of crustose species to settle, while increasing settlement of those species that live within algal beds. This has been observed

in MPAs along the south and east coast of South Africa, where protected rocky shores have a higher abundance of sessile fauna e.g. barnacles and mussels while those that are associated with algal mats are more abundant at harvested sites (Lasiak & Field 1995). Similar to these studies, the harvested sites I surveyed (Wireless Point and Kommetjie) were dominated by extensive mats of *Ulva* spp., *Pachymenia orbitosa* and *Mazzaella capensis*. This is most likely due to the depletion of limpets such as *C. granatina* (and, at Wireless Island, *S. argenvillei*), which has created opportunities for the growth of opportunistic algae like *Ulva* spp. (Lasiak & Field 1995, Lasiak 1998, 1999, Deepananda & Macusi 2012). The dominance of a single genus (*Ulva*) in the community composition of Wireless Point while at the other harvested site, Kommetjie, *P. orbitosa* and *Sarcothalia stiriata* were abundant suggests different degrees of disturbance between these sites, as I outlined above. In addition, dominance by *Ulva* spp. indicates an altered interaction between herbivores and algae, with shellfish-gathering leading to increased abundance of algal mats, while protection against shellfish harvesting strengthens the limpet/algal interaction, as was reflected by the rarity of opportunistic species at the Scarborough sites. Increased algal growth might have knock-on consequences for the functioning of the ecosystem, including reduced feeding and altered settlement of mussels, and smothering of other organisms through overgrowth by algae (Lasiak & Field 1995, Lasiak 1998, 1999, Deepananda & Macusi 2012).

The abundances and contributions of taxa to differences in community composition provide information on the state of the habitat (Lasiak & Field 1995, Lasiak 1999). The differences in community composition between sites that experience high versus low harvesting pressure are usually due to commonly harvested species being abundant in protected sites, whereas at harvested sites algae and algal-associated species become distinguishing taxa (Lasiak & Field 1995, Lasiak 1998, 1999). For example, Deepananda & Macusi (2013) reported dominance of opportunistic algal species such as *Gracilaria cassa*, *Valoniopsis pachynema* and *Padina boergesenii* in the community composition of harvested sites in Sri Lanka. Hence, the abundance of *Ulva* spp., an opportunistic species, at the harvested sites I examined was not surprising, as similar patterns have been observed elsewhere in South Africa and worldwide in areas where grazers have been depleted (Dye 1993, 1995, Lindberg et al. 1998, Micheli et al. 2005, Maneveldt et al. 2009, Martins et al. 2010a, Almeida et al. 2016, Riera et al. 2016). The greater abundances of *C. granatina* and *S. argenvillei* among species that distinguish the protected sites I surveyed (Scarborough North and South) indicates direct benefits of protection

through this MPA. Similarly, the higher contributions of *M. galloprovincialis* to community composition at the protected Scarborough sites showed that this alien species is (ironically) also benefitting from the protection in the no-take sections of the MPA. The greater contributions of *Chamberlainium* spp. at the two protected sites reflect a strong association between *Chamberlainium* spp. and *Scutellastra cochlear* (Maneveldt & Keats 2008), as average densities of this limpet were also greater in the protected sites, even although it is not harvested. It is also a reflection of the positive association between encrusting coralline algae and limpets as a whole (Steneck 1986, Dethier & Steneck 2001), which Blamey & Branch (2009) have demonstrated elsewhere on the west coast of South Africa.

### *Spatial differences in densities of key species*

As mentioned, protection level plays a major role in determining the densities of the commonly harvested *C. granatina* and *S. argenvillei*. The higher densities of the commonly harvested *C. granatina* in the Scarborough no-take area compared to the harvested Wireless Point and Kommetjie sites indicates that this species is benefiting from the greater protection in the no-take areas, as has been demonstrated for limpet populations elsewhere (Branch & Odendaal 2003, Lasiak 2006, Rius & Zabala 2008, Bednar & Trulio 2017). The case for *S. argenvillei* is less clear-cut, as its abundances were greater at only one of the protected sites (although its sizes were greater at both protected sites). The four to 15-fold differences in densities of *C. granatina* that I recorded indicate that the reserve succeeds in maintaining the exceptionally high natural densities that this species achieves in other unharvested parts of the west coast (Bustamante et al 1995a); and this is probably true for *S. argenvillei* as well. Similarly, higher densities have been reported for *C. oculus* (Lasiak 1991b, Branch & Odendaal 2003), *Perna perna* (Rius et al. 2006) and *S. longicosta* (Lasiak 1991b) in marine protected areas on the south-east coast of South Africa, and for *Patella ferruginea* in Sinis-Isola MPA, Italy (Coppa et al. 2015), following exclusion of harvesting from rocky shores.

The lack of protection effects on *S. granularis* was expected as this species is rarely harvested and did not occur among the species collected by harvesters (see Chapter 2). The low density of *S. granularis* at Wireless Point compared to Kommetjie and Scarborough South was, however, unexpected. Density of this species is enhanced in areas with a high cover of *M.*

*galloprovincialis*, due to improved recruitment and survival on the secondary space provide by the mussel's shells (Griffiths et al. 1992, Robinson et al. 2007, Branch et al. 2008, 2010, Sadchatheeswaran et al. 2015). In my study, *S. granularis* was always common on the shells of the *M. galloprovincialis*, which was abundant at Scarborough South but almost absent from Wireless Point. Differences in the abundance of *S. granularis* may therefore be a secondary effect of the relative abundance of *M. galloprovincialis*, and unrelated to differences in harvesting. Although harvesting may contribute to the scarcity of *M. galloprovincialis* at Wireless Point, a more likely explanation is that this site lies in the lee of Wireless Island and therefore experiences less wave action. The abundance of *M. galloprovincialis* is strongly linked to wave action, which supplies particulate food material for the mussel (Bustamante & Branch 1996b). However, the reasons for the high abundance of *S. granularis* at Kommetjie where *M. galloprovincialis* was also scarce remains unclear.

### *Spatial differences in shell lengths of key species*

As noted above, it is common practice for harvesters to select large individuals. Consequently, mean sizes of targeted species tend to diminish on harvested rocky shores (Hockey & Bosman 1986, Lasiak 1991a, 1991b, 1998, Branch & Odendaal 2003, Kido & Murray 2003, Roy et al. 2003, Sagarin et al. 2007, Jimenez et al. 2011, Fenberg & Roy 2012). The presence of larger shell lengths of *C. granatina* and *S. argenvillei* at the Scarborough sites than at the harvested sites of Kommetjie and Wireless Point accords with size-selective harvesting by humans (see Chapter 2). This is not surprising, as highly exploited limpets species often demonstrate a truncated shell size distribution (Hockey & Bosman 1986, Lasiak 1991b, 1992, 1993a, Pombo & Escofet 1996, Branch & Odendaal 2003, Kido & Murray 2003, Roy et al. 2003, Sagarin et al. 2007, Fenberg & Roy 2012). The argument that harvesting is the root cause of this pattern in these species is strengthened by the fact that the rarely harvested *S. granularis* did not exhibit a reduction of size in harvested areas: indeed, its sizes at one of the harvested sites, Wireless Point, were 12-19% greater than at either of the protected Scarborough sites. The differences in shell lengths of *C. granatina* and *S. argenvillei* translate to 8-12% declines, falling within the range of declines reported for other molluscan populations under intense harvesting pressure: e.g. 8.6-10% for *Anadara scapha*, *Gafrarium tumidum* and *Modiolus auriculatus* in New Caledonia (Jimenez et al. 2011, 2015), 20-30% for *C. oculus* in South Africa (Branch &

Odendaal 2003) and 28% for *Lottia gigantea* in California (Kido & Murray 2003). Archaeological middens testify to the fact that such effects extend back to prehistoric times exceeding 100 000 years before present (e.g., Jerardino 2012, Parkington et al. 2013).

### *Correlations between limpet densities and algal cover*

The negative correlation that emerged between limpets and ephemeral algae is not new: many previous studies have shown that removal of limpets increases ephemeral algae (Lodge 1948, Babcock et al. 2010, Aguilera & Navarrete 2012). In my study, the highest abundances of algae were observed at Wireless Point where there were relatively few limpets compared to Kommetjie and the Scarborough sites. The overall relationship between limpet abundance and percentage cover of corticated algae was however unexpected, exhibiting an initial increase in algal cover as limpet densities rose, and then declining again at higher limpet densities. It is, however, possible the 'intermediate disturbance hypothesis' (Connell 1978) plays a role in explain this pattern, with greater competition from ephemerals reducing abundance of corticated algae at low limpet densities, and intensified grazing reducing them at high limpet densities.

The positive correlation between encrusting algae (dominated by *Chamberlainium* spp.) and limpets, particularly *Scutellastra cochlear* (Maneveldt et al. 2006) is probably partially fuelled by the release of nutrients by *S. cochlear*, which are taken up by the surrounding algal 'gardens' this limpet occupies (Plagányi & Branch 2000). Encrusting algae constitute 80% of the diet of this limpet, and grazing intensity on the thalli promotes their growth rate (Keats et al. 1994, Maneveldt & Keats 2008). In addition, grazing promotes encrusting corallines because it prevents competitive overgrowth by foliar algae (Steneck 1986). Steneck (1982) reported that the encrusting alga *Clathromorphum circumscriptum* reached highest percentage cover in areas with high densities of *Acmaea testudinalis*, and argued mutual inter-dependency between these species. Maneveldt & Keats (2008) noted an absence of encrusting algae in the lower zones of west-coast areas where ever *S. cochlear* is absent. Bulleri et al. (2000) observed a similar positive relationship between encrusting algae and *Patella aspera* in Italy. This strengthens the argument that encrusting algae benefit from the coexistence with grazers, particularly *S. cochlear* in this case.

Encrusting coralline algae have been shown to be preferential settlement sites for a range of invertebrates, including abalone *Haliotis* spp. (Morse & Morse 1984) and the commercially important *H. midae* in particular (Tarr et al. 1996, Day & Branch 2000, 2002). Reductions in the abundance of grazers, with resultant effects on encrusting corallines, are therefore of more than academic interest.

## Conclusions

The community composition on the rocky shores of Wireless Island and Wireless Point has changed considerably between 1970 and 2017. These changes were driven by the arrival and spread of the alien mussel *M. galloprovincialis*, coupled with intensification of harvesting. Harvesting has decimated the populations of *C. granatina* and, to a lesser extent, *S. argenvillei*, and reduced the average size of individuals of both species at the two harvested sites I examined. In turn, this has led to increases in macroalgal cover, particularly at Wireless Point where ephemeral algae have overrun the rocky shores.

Arrival of the alien mussel *M. galloprovincialis* has, over time, changed the abundance of *S. granularis* in different zones, leading to a reversal in the previous density- and size-zonation patterns at Wireless Island. In my spatial comparison of sites, the community composition differed between the protection levels and among sites, with communities inside no-take areas being dominated by the commonly harvested taxa *C. granatina*, *M. galloprovincialis* and *S. argenvillei*, whereas at the two harvested sites, Kommetjie and Wireless Point, communities were characterised by greater abundances of algae and the rarely harvested limpets *S. granularis*, reflecting the direct and indirect impacts of harvesting versus protection on rocky shores. In addition, whereas harvesting at Kommetjie and Wireless Point led to lower population densities and smaller sizes of commonly harvested limpets than at the protected Scarborough sites, the rarely harvested *S. granularis* did not differ in any systematic way in density or size between the harvested and protected sites, suggesting that harvesting is indeed the driving factor of the observed differences between the restricted and controlled zones of the TMNP MPA.

# Chapter 4: Effects of experimental harvesting of a key grazer *Cymbula granatina* on rocky shore community composition


## Abstract

Densities of the commonly-harvested intertidal limpet *Cymbula granatina* were manipulated at two sites within a no-take marine protected area using four treatment levels ranging from zero to maximum natural densities, to evaluate the effects of different harvesting intensities of this limpet on rocky shore community composition. Following removal or thinning of *C. granatina*, community composition changed, cover of corticated and ephemeral algae increased and recruitment of *C. granatina* decreased. These outcomes were, however, dependent on the time frame considered, as algae underwent an annual cycle, and the effects of limpet removal were evident predominantly during the upwelling season when the algae proliferated. The management implications of the results of this experiment are discussed.


## Introduction

Patellid limpets are commonly faced with overexploitation due to harvesting for food or for commercial purposes (Hockey & Bosman 1986, Oliva & Castilla 1986, Hockey et al. 1988, Lasiak & Field 1995, Lasiak 1998, 1999, Coppa et al. 2012, 2015). As keystone grazers, they also play a central role in structuring community composition, and their loss may alter the ecosystem through direct or indirect effects on other species (Dye 1995, Maneveldt et al. 2009, Crowe et al. 2011, Borges et al. 2015). However, the nature of changes in community composition may differ depending on the role of particular species in the community, and therefore needs to be evaluated for each species and habitat, and must account for the intensity at which harvesting is occurring, as this may differ among areas (Borges et al. 2015).

Removal of limpets often causes an increase in the dominance of rocky shores by algae (e.g. Dye 1995, Maneveldt et al. 2009, Borges et al. 2015). In addition to such grazing effects, limpets hinder other species from becoming established by 'bulldozing' early life stages; and because of this, limpet removal has been associated with an increase in mussel and barnacle recruitment (Dayton 1971, Steffani & Branch 2005, Menge et al. 2010). Harvesting limpets thus has profound effects on non-targeted organisms due to associated reductions in grazing pressure, disturbance and competition for space (Dye 1995, Steffani & Branch 2003, 2005, Branch et al. 2008, 2010, Maneveldt et al. 2009, Crowe et al. 2011, Borges et al. 2015, Ellrich et al. 2020). Indirect negative effects of a reduction in grazing pressure include greater

mortality of barnacles and encrusting algae due to smothering caused by overgrowth by algae (Steneck 1982, Farrell 1988, Maneveldt & Keats 2008, Tejada-Martinez et al. 2016). Depletion of limpets may also have adverse effects on birds that prey on them, even being a likely contributor to the extinction of the Canarian black oystercatcher *Haematopus meadewaldoi* (Hockey 1987). Limpets may also compete with mussels and other grazers for space and their competitors can benefit if limpets are depleted (Branch et al. 2008, 2010, Maneveldt et al. 2009). For example, in South Africa, space left behind by removal of the limpet *Scutellastra argenvillei* has been taken over by the alien mussel *M. galloprovincialis* (Branch et al. 2008, 2010); and removal of the limpet *Cymbula oculus* also resulted in increased invasion of the intertidal zone by *M. galloprovincialis* (Maneveldt et al. 2009). Thus, removal of limpets can have far reaching consequences for other species, and may alter ecosystems in numerous ways.

*Cymbula granatina* is a dominant herbivore on rocky shores of the west coast of South Africa where it forms dense low-diversity beds in the mid to low intertidal zones of sheltered and semi-exposed rocky shores (Eekhout et al. 1992, Bustamante et al. 1995a). Its large size and accessibility make it one of the most commonly harvested limpets and some populations have become decimated by harvesting (Eekhout et al. 1992, Griffiths & Branch 1997), even in archaeological eras (Parkington et al. 2013). This species has the potential to be a key component influencing ecosystem function in the region, so over-harvesting is a cause for concern. *Cymbula granatina* has a complex feeding behaviour, beginning its post-larval life as a grazer and switching to trapping drift algae as an adult, which further complicates its impacts on communities and the effects of its depletion by harvesting. In the light of efforts to introduce ecosystem-based management to fisheries, understanding the impacts of exploitation on the whole ecosystem has emerged as an important goal, and assessments of the effects of different levels of harvesting intensity on other rocky shore populations and the entire community are needed to devise suitable management strategies.

The Table Mountain National Park (TMNP) Marine Protected Area (MPA) offers an opportunity to examine the effects of removing *C. granatina* on the community composition of rocky shores. Populations of *C. granatina* reach high densities in no-take areas as a result of protection from exploitation, which can be compared with ‘controlled’ zones within the Park, where harvesting may take place but is regulated in accordance with national policies and laws.

In this chapter, I address the impacts of harvesting *C. granatina* by manipulating its densities and observing consequent changes in community composition over the course of 1.5 years. Five hypotheses were tested: (1) Community composition will change following the removal or thinning of *C. granatina*, and the magnitude of the effect will be related to the proportion of limpets removed. (2) Corticated and ephemeral algae will increase as a result of reduced grazing, leading to a reduction in bare rock, both responses again being related to the proportions of limpets removed. (3) Encrusting algae will decrease following removal or thinning of *C. granatina* because increased macroalgal cover will smother crusts. (4) The abundances of recruits of *C. granatina* will increase in areas with lower densities of *C. granatina* adults because of a reduction in the intensity of grazing and competition for space. (5) Other grazers will also invade areas with no or few *C. granatina* because of reduced competition.

## Materials and methods

The study was conducted on intertidal rocky shores at two sites, named Scarborough North and Scarborough South (see Fig. 3.1 in Chapter 3), which are both formally protected from human harvesting and support dense populations of *C. granatina*. Spring tidal range in the region is ca. 1.8 m, and experimental plots were placed between mid-tide and low-tide levels where *C. granatina* is most abundant. Both sites are situated on a wave-exposed coastline, but the locations of the experimental plots were relatively sheltered from the direct impact of waves by seaward rock ledges and outcrops, making them sheltered to semi-exposed – a habitat that is typical of the species (Bustamante et al. 1995a).

### *Experimental design*

To evaluate the effects of variable densities of *C. granatina* on rocky shore communities, a herbivore exclusion experiment was set up in November 2017, in which this limpet was excluded or thinned to fixed proportions of normal densities inside 30 x 30-cm plots. To simulate different levels of exploitation and control for potential side effects arising from the experimental procedure, the experiment had three types of exclusion treatments: a cage treatment (C), a semi-fenced treatment (SM) and an unfenced treatment (U), with treatments having four density levels that were each replicated four times (Fig. 4.1). The levels were: (a)

100% of natural densities (>12 individuals/plot, control) where no reduction of density was undertaken, (b) 50% (7-9 individuals/plot, lightly harvested), (c) 10% (single limpet/plot, heavily harvested) and (d) 0% (no limpets/plot, depleted). These levels are henceforth referred to as C100, C50, C10 and C0, respectively, for the cage treatment. Equivalent densities were established for the unfenced treatment. The semi-fenced (SM) treatment had two density levels only, 100% (SM100) and 0% (SM0) of natural densities of *C. granatina* because of time constraints on sampling during low tide and because I assumed that examining the extremes of density would be sufficient to test for caging effects. The total number of experimental units was thus 40 per site, for 10 treatment/density combinations. The use of three exclusion methods allowed me to control for possible caging effects, such as any influence of the caging materials and of wave reduction. Specifically, cages vs. semi-fences were compared to test for wave-reduction effects, and semi-fences vs. unfenced to test for cage-material effects.

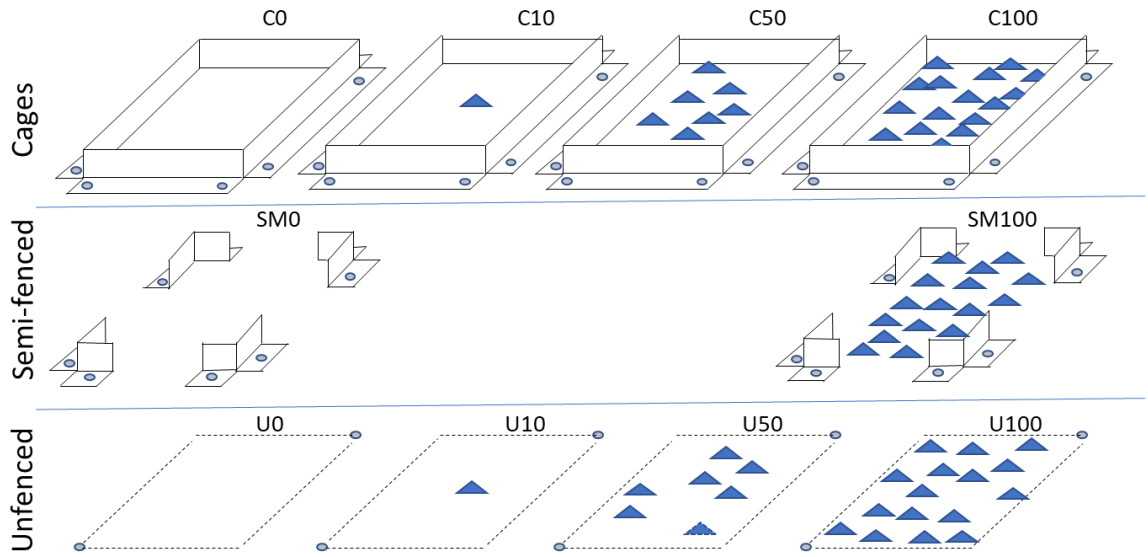



Figure 4.1 Schematic diagram of the experimental set up showing different exclusion methods by which densities of *C. granatina* (blue triangles) were manipulated: full enclosures represent cages (C), enclosures with broken sides illustrate semi-fences (SM) and dotted lines represent unfenced open plots (U) marked only by bolts (small circles). Each treatment was replicated four times at each of two sites.

Stainless steel angle-iron strips of 5-mm thickness, 5 cm tall and 30 cm long were installed on the rocks to form square enclosures, or cages, by drilling into the rock and attaching the angle iron with stainless steel screws and washers. Cage treatments thus completely surrounded

limpets of the specified densities to enclose them while preventing, or at least limiting, other limpets from entering (Fig. 4.1). In the semi-fenced treatments, corners of angle iron were installed to mark the corners of plots so that limpets were free to move in and out of the plots, but any effect that the angle iron might have had on wave exposure could be assessed. Unfenced plots did not employ any angle iron, and had only corners marked with two bolts placed diagonally. They served as controls to assess any effect the caging materials might have had on the experiment, as outlined above. Plots were serviced twice a month when possible and, on each occasion, limpets that had entered the plot were removed, or if any had disappeared from the plots, additional limpets were added to maintain the intended density levels. All three exclusion methods proved effective in maintaining the densities of adults of *C. granatina*, as they tend to occupy fixed positions and obtain food by trapping drift algae (Bustamante et al. 1995a); but juveniles (individuals < 40 mm length) did move in and out of plots, with the 'cage' treatment being most effective and the unfenced 'open' plots least effective in controlling their movements. The use of stainless-steel fences was preferred over roofed cages to minimise shading effects, and they were also preferred over antifouling paint because of the toxic effects of the latter.

In all experimental units, the percentage cover of each sessile species and the numbers of mobile organisms were recorded approximately monthly on 13 occasions spanning 18 months, and photographs taken of plots on each occasion. Sample dates are referred to as T1, T2, T3 etc., with T1 being the start date in November 2017, through to T13 in June 2019. Specific months in which monitoring was undertaken are indicated in the Results. Numbers of mobile species were later converted to percentage cover following methods used by Wieters et al. (2009), so that analyses were based on percentage cover, including a measure of 'bare rock' (which included space on top of *C. granatina* shells)'. To assess the effects of *C. granatina* on the composition of the rest of the community, this species was excluded from the community dataset. Total percentage cover could exceed 100% because of secondary growth of some organisms on others. The species were grouped into nine functional groups for analyses of community composition (Table 4.1).

**Table 4.1.** The functional groups to which algae and invertebrate species were assigned in this study, modified from Wieters et al. 2009.

| **Ephemeral algae** | **Corticated algae** | **Articulated algae** | **Mussels** | **Patellid limpets** | **Whelks** |
|---|---|---|---|---|---|
| *Callithamnion collabens* | *Brassicophycus* | *Arthrocardia* spp. | *Aulacomya atra* | *Cymbula oculus* | *Burnupena catarrhacta* |
| *Caulacanthus* spp. | *brassicaeformis* | *Cheilosporum* spp. | *Mytilus galloprovincialis* | *Scutellastra argenvillei* | *Burnupena cincta* |
| *Centroceras* spp. | *Champia lumbricalis* | *Corallina* spp. | | *Scutellastra barbara* | *Burnupena lagenaria* |
| *Ceramium* spp. | *Chordariopsis capensis* | *Jania* spp. | **Other filter feeders** | *Scutellastra cochlear* | *Burnupena papyracea* |
| *Chaetomorpha* spp. | *Chylocladia capensis* | | *Crepidula porcellana* | *Scutellastra granularis* | |
| *Cladophora* spp. | *Gelidium micropterum* | | *Dendropoma corallinaceus* | *Scutellastra longicosta* | |
| *Porphyra* spp. | *Gelidium pristoides* | **Algal crusts** | *Dodecaceria pulchra* | | |
| *Ulva* spp. | *Gelidium reptans* | *Black crust* | *Hymeniacidon perlevis* | **Other grazers** | |
| | *Gigartina polycarpa* | *Ralfsia verrucosa* | *Gunnarea gaimardi* | *Acanthochitona garnoti* | |
| | *Gymnogongrus dilatatus* | *Chamberlainium* | *Pyura stolonifera* | *Chiton polita* | |
| | *Leathesia marina* | spp. | | *Fissurella* spp. | |
| | */Colpomenia sinuosa* | | | *Helcion dunkeri* | |
| | *Mazzaella capensis* | | | *Helcion pectunculus* | |
| | *Nothogenia ovalis* | | | *Oxystele antoni* | |
| | *Pachymenia orbitosa* | | | *Oxystele tigrina* | |
| | *Sarcothalia stiriata* | | | *Oxystele sinensis* | |
| | *Splachnidium rugosum* | | | *Oxystele impervia* | |
| | | | | *Parechinus angulosus* | |
| | | | | *Siphonaria capensis* | |
| | | | | *Siphonaria concinna* | |
| | | | | *Siphonaria* spp. | |

### *Data analyses*

A summary of all comparisons made, including tests for experimental artefacts and density treatments effects is shown in Table 4.2.

**Table 4.2.** Experimental controls conducted through comparisons among the three different exclusion methods (C = cages; SM = semi-fences; U = unfenced) and among density manipulations of *C. granatina* (100%, 50% 10% 0%).

| **Comparisons between treatments** | **Effect examined** |
|---|---|
| C100 vs SM100; U100 vs SM100; C100 vs U100; | Cage effects |
| C50 vs U50; C10 vs U10; C0 vs U0; C0 vs SM0; U0 vs SM0 | |
| C100 vs C50; C100 vs C10; C100 vs C0; | Effect of limpet density in the cages |
| C50 vs C10; C50 vs C0; C10 vs C0 | |
| U100 vs U50; U100 vs U10; U100 vs U0; | Effect of limpet density in the unfenced treatments |
| U50 vs U10; U50 vs U0; U10 vs U0 | |
| SM100 vs SM0 | Effect of limpet density in the semi-fenced treatments |

A four-way Repeated Measures PERMANOVA with site, exclusion method, density level as independent (fixed) factors and time as repeated (fixed) factor was conducted on the functional-group percentage-cover data to determine whether equivalent exclusion methods (cage, semi-fence control, unfenced control) had different effects on the community composition, i.e., if there were cage effects. Initial analyses showed that (a) responses were different at the two sites ($P < 0.05$); and (b) similar to findings of Daza-Guerra et al. (2020), cage effects were rare, with community composition not being statistically different among comparable limpet densities in cages, semi-fence controls and unfenced controls in 94% of the comparisons; $P > 0.05$ in all cases (Tables 4.3A, B). I was therefore confident that cage effects did not influence the results to any material extent and subsequently focused on results from the cage treatments only, as they were most effective in maintaining the desired limpet densities.

To determine the effects of thinning *C. granatina* densities on community composition in the caged treatment, a three-way Repeated Measures PERMANOVA with site and density as independent (fixed) factors and time as repeated (fixed) factor was applied after the data were standardised (by sample) by dividing the percentage cover of each functional group by the total cover in each quadrat and multiplying by 100. Standardised values were then square-root transformed for Repeated Measures PERMANOVA and portrayal in MDS plots. Significant effects were explored using pairwise post-hoc comparison tests. SIMPER analyses were used to identify the functional groups responsible for any differences in communities among limpet densities, of which I report only groups that contributed >10% to the cumulative 90% of dissimilarities between density treatments. To further explore patterns, changes in the densities and percentage cover of various individual functional groups were evaluated using three-way Repeated Measures ANOVAs (with site and density as independent factors and time as repeated factor). The data were first tested for normality and heterogeneity of variance using Shapiro-Wilk and Levene's tests respectively and, where necessary, data were square-root transformed to meet the ANOVA assumptions. To determine relationships between functional groups and *C. granatina* densities, quantile regressions were used because they are robust for wedge-shaped data distributions that are characterised by outliers, and because the data did not meet assumptions of normality and heterogeneity of variance even after transformation (Cook & Manning 2013, Yirga et al. 2018, Wei et al. 2019).

**Table 4.3A**. Pairwise comparison of 4-way Repeated Measures PERMANOVAs with factors site, treatment, density and time, contrasting functional-group community composition between exclusion methods at four equivalent densities over time (November 2017 to June 2019) at Scarborough North. Bold values indicate significantly different community composition. U = unfenced; SM = semi-fenced; C = caged. 100 = control density of *C. granatina* of 100%; 50 = density reduced to 50%; 10 = density reduced to 10%; 0 = zero density.

| Groups | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **U100, SM100** | T= 1.057 | T= 1.539 | T= 1.570 | T= 1.717 | **T= 2.156** | **T= 2.130** | T= 0.946 | T= 1.39 | T= 1.497 | **T= 1.787** | **T= 2.379** | T= 0.822 | T= 0.485 |
| | P= 0.509 | P= 0.152 | P= 0.083 | P= 0.093 | **P= 0.037** | **P= 0.023** | P= 0.556 | P= 0.053 | P= 0.055 | **P= 0.033** | **P= 0.027** | P= 0.92 | P= 0.926 |
| **U0, SM0** | T= 3.026 | T= 1.059 | T= 1.826 | T= 1.267 | **T= 1.814** | T= 2.251 | T= 0.672 | T= 0.871 | T= 1.610 | T= 1.559 | T= 0.988 | T= 1.044 | T= 1.363 |
| | P= 0.056 | P= 0.318 | P= 0.065 | P= 0.22 | **P= 0.045** | P= 0.067 | P= 0.786 | P= 0.418 | P= 0.094 | P= 0.075 | P= 0.374 | P= 0.325 | P= 0.162 |
| **C100, SM100** | T= 1.026 | T= 1.029 | T= 1.569 | T= 1.190 | T= 1.073 | T= 0.573 | T= 1.179 | T= 0.961 | T= 1.153 | T= 0.889 | T= 0.605 | T= 1.116 | T= 0.275 |
| | P= 0.365 | P= 0.506 | P= 0.075 | P= 0.292 | P= 0.401 | P= 0.885 | P= 0.237 | P= 0.556 | P= 0.354 | P= 0.639 | P= 0.822 | P= 0.167 | P= 0.956 |
| **C0, SM0** | T= 1.156 | T= 1.349 | T= 0.918 | T= 1.281 | T= 0.911 | T= 1.0159 | T= 1.077 | T= 1.200 | T= 1.254 | T= 1.383 | T= 2.126 | T= 0.816 | T= 0.722 |
| | P= 0.224 | P= 0.213 | P= 0.465 | P= 0.246 | P= 0.465 | P= 0.403 | P= 0.293 | P= 0.208 | P= 0.275 | P= 0.167 | P= 0.058 | P= 0.533 | P= 0.639 |
| **C100, U100** | T= 1.037 | T= 1.308 | T= 1.035 | T= 1.858 | **T= 1.946** | T= 1.753 | T= 1.169 | T= 1.653 | T= 1.351 | T= 1.353 | T= 1.980 | T= 1.736 | T= 0.349 |
| | P= 0.389 | P= 0.169 | P= 0.505 | P= 0.133 | **P= 0.034** | P= 0.056 | P= 0.369 | P= 0.056 | P= 0.17 | P= 0.197 | P= 0.094 | P= 0.103 | P= 0.88 |
| **C50, U50** | T= 1.637 | T= 1.637 | **T= 2.618** | T= 0.854 | T= 1.050 | T= 0.941 | T= 1.001 | T= 1.064 | T= 0.939 | T= 1.404 | T= 0.404 | T= 0.768 | T= 0.984 |
| | P= 0.146 | P= 0.146 | **P= 0.038** | P= 0.621 | P= 0.338 | P= 0.524 | P= 0.463 | P= 0.396 | P= 0.423 | P= 0.183 | P= 0.818 | P= 0.623 | P= 0.465 |
| **C10, U10** | T= 1.286 | T= 0.310 | T= 0.920 | T= 0.575 | T= 0.213 | T= 0.771 | T= 0.702 | T= 0.651 | T= 0.737 | T= 0.988 | T= 0.897 | T= 0.297 | T= 0.215 |
| | P= 0.215 | P= 0.943 | P= 0.542 | P= 0.874 | P= 0.973 | P= 0.489 | P= 0.648 | P= 0.765 | P= 0.635 | P= 0.374 | P= 0.454 | P= 1 | P= 0.975 |
| **C0, U0** | T= 1.444 | T= 0.984 | T= 1.268 | T= 0.841 | T= 1.105 | T= 1.452 | T= 0.315 | T= 0.857 | T= 1.476 | T= 1.414 | T= 1.694 | T= 1.178 | T= 1.082 |
| | P= 0.186 | P= 0.39 | P= 0.353 | P= 0.507 | P= 0.377 | P= 0.253 | P= 0.942 | P= 0.511 | P= 0.278 | P= 0.226 | P= 0.12 | P= 0.273 | P= 0.387 |

**Table 4.3B**. Pairwise comparison of 4-way Repeated Measures PERMANOVAs with factors site, treatment, density and time, contrasting functional-group community composition between exclusion methods at four equivalent densities over time at Scarborough South. Empty cells indicate comparisons that were not possible due to missing data. Bold values indicate significantly different community composition. U = unfenced; SM = semi-fenced; C = caged. 100 = control density of *C. granatina* of 100%; 50 = density reduced to 50%; 10 = density reduced to 10%; 0 = zero density.

| Groups | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **U100, SM100** | T= 0.684 | **T= 2.138** | T= 1.131 | T= 1.256 | T= 1.292 | T= 0.958 | T= 0.827 | T= 1.125 | T= 0.996 | T= 0.932 | T= 0.487 | T= 1.323 | T= 0.931 |
| | P= 0.742 | **P= 0.028** | P= 0.344 | P= 0.258 | P= 0.207 | P= 0.47 | P= 0.541 | P= 0.286 | P= 0.429 | P= 0.569 | P= 0.921 | P= 0.278 | P= 0.627 |
| **U0, SM0** | T= 2.310 | **T= 3.098** | T=2.378 | **T= 2.787** | T= 2.503 | T= 2.691 | T= 2.211 | T= 2.819 | T= 1.370 | T= 2.948 | | T= 2.337 | T= 1.327 |
| | P= 0.088 | **P= 0.033** | P= 0.103 | **P= 0.023** | P= 0.092 | P= 0.073 | P= 0.058 | P= 0.065 | P= 0.255 | P= 0.064 | | P= 0.151 | P= 0.189 |
| **C100, SM100** | | T= 0.158 | T= 0.517 | T= 0.970 | T= 0.614 | T= 0.231 | T= 1.201 | T= 0.711 | T= 0.484 | T= 1.318 | T= 0.879 | T= 0.416 | T= 0.495 |
| | | P= 0.963 | P= 0.932 | P= 0.413 | P= 0.668 | P= 0.97 | P= 0.292 | P= 0.553 | P= 0.766 | P= 0.184 | P= 0.509 | P= 0.915 | P= 0.719 |
| **C0, SM0** | T= 1.033 | T= 0.965 | T= 0.728 | T= 0.902 | T= 0.811 | T= 1.277 | T= 0.944 | T= 0.848 | T= 1.081 | T= 0.711 | | T= 0.479 | T= 0.736 |
| | P= 0.374 | P= 0.357 | P= 0.647 | P= 0.36 | P= 0.477 | P= 0.279 | P= 0.534 | P= 0.464 | P= 0.373 | P= 0.479 | | P= 0.598 | P= 0.641 |
| **C100, U100** | T= 0.337 | T= 0.965 | T= 0.717 | T= 1.739 | T= 1.297 | T= 1.096 | T= 1.798 | T= 1.224 | T= 1.063 | T= 2.009 | | T=1.511 | |
| | P= 0.942 | P= 0.508 | P= 0.728 | P= 0.087 | P= 0.198 | P= 0.285 | P= 0.118 | P= 0.188 | P= 0.394 | P= 0.120 | | P= 0.156 | |
| **C50, U50** | **T= 2.559** | T= 0.835 | T= 0.935 | T=0.533 | T= 0.908 | T= 0.799 | T= 0.561 | T= 0.770 | T= 1.219 | **T= 2.127** | T= 0.707 | T= 0.143 | T= 0.734 |
| | **P= 0.023** | P= 0.504 | P= 0.418 | P= 0.918 | P= 0.565 | P= 0.537 | P= 0.783 | P= 0.573 | P= 0.251 | **P= 0.039** | P= 0.668 | P= 0.966 | P= 0.586 |
| **C10, U10** | T= 0.889 | T= 0.765 | T= 1.290 | T= 1.037 | T= 1.295 | T= 0.577 | T= 0.585 | T= 0.535 | T= 1.191 | T= 1.269 | T= 0.725 | T= 1.330 | T= 0.947 |
| | P= 0.455 | P= 0.645 | P= 0.259 | P= 0.416 | P= 0.175 | P= 0.982 | P= 0.822 | P= 0.968 | P= 0.240 | P= 0.138 | P= 0.974 | P= 0.056 | P= 0.447 |
| **C0, U0** | T= 1.260 | T= 1.980 | T= 1.487 | T= 1.570 | **T= 1.916** | T= 1.304 | T= 1.559 | T= 1.945 | T= 1.494 | T= 2.061 | T= 1.491 | T= 1.913 | T= 0.952 |
| | P= 0.268 | P= 0.091 | P= 0.15 | P= 0.15 | **P= 0.026** | P= 0.258 | P= 0.112 | P= 0.074 | P= 0.204 | P= 0.081 | P= 0.135 | P= 0.077 | P= 0.523 |

# Results

*Effects of limpet density on community composition*

Focussing solely on the cage treatment for reasons stated in the Methods, a three-way Repeated Measures PERMANOVA revealed a significant main effect of time on the community composition (Table 4.4), as well as a significant interaction of site and density, indicating that the effects of removing limpets on the community composition differed between the two sites. For further analyses I therefore considered the two sites separately.

**Table 4.4.** Results of three-way Repeated Measures PERMANOVA testing for the effects of site, limpet density and time, as well as their interactions, on community composition. Asterisks indicate significant results ($p < 0.05$).

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| Site | 1 | 20769 | 20769 | 28.45 | < 0.01* |
| Density | 3 | 106725 | 35573 | 48.73 | < 0.01* |
| Time | 12 | 28422 | 2368.50 | 3.24 | < 0.01* |
| Site: Density | 3 | 22291 | 7430.40 | 10.18 | <0.01* |
| Site: Time | 11 | 5822.7 | 485.22 | 0.67 | 0.89 |
| Density: Time | 36 | 12084 | 335.67 | 0.46 | 1 |
| Site: Density: Time | 36 | 8225.3 | 228.48 | 0.31 | 1 |
| Residuals | 311 | 227055 | 730.06 | | |

At the start of the experiment (T1), community compositions at both sites did not differ among reduced-density (C0, C10, C50) and full density (C100) treatments (Table 4.5). Thereafter, pairwise comparisons reflected interactions between site and density. At Scarborough North, community composition in C10 began to diverge from C100 after five months (T5), and differences between reduced and natural density treatments were evident again at T8, T11 and T12. Few other significant differences emerged, apart for C100 vs. C0 at time T8, and C50 vs. C10 at T2.

At Scarborough South, the differences between C10 and C100 densities were pervasive from T4 through to T12. Other density levels rarely resulted in differences from natural densities, but significant differences between C50 and C100 did emerge once at T10, between C50 and C10 at T5, T9 and T12, and between C0 and C10 at T9. Surprisingly, significant differences between C0 (in which limpets were completely removed) and C100 appeared on only one occasion, at Scarborough North at T8.

**Table 4.5**. Pairwise comparison of 3-way Repeated Measures PERMANOVAs, contrasting community composition between paired densities in caged treatments over time, spanning November 2017 to June 2019. Bold values indicate significant different community composition.

| | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Scarborough North** | | | | | | | | | | | | | |
| **C100, C50** | T= 0.519 | T=1.093 | T= 0.488 | T= 1.381 | T= 1.399 | T= 0.449 | T= 0.992 | T= 1.096 | T= 0.799 | T= 0.633 | T= 0.971 | T= 1.736 | T= 0.843 |
| | P= 0.779 | P= 0.325 | P= 0.929 | P= 0.195 | P= 0.127 | P= 0.948 | P= 0.521 | P= 0.343 | P= 0.596 | P= 0.681 | P= 0.494 | P= 0.066 | P= 0.64 |
| **C100, C10** | T= 1.823 | T= 1.971 | T= 1.257 | T= 2.230 | **T= 2.344** | T= 1.866 | T= 2.437 | **T= 2.515** | T= 2.369 | T= 2.050 | **T= 2.079** | **T= 4.318** | T= 2.303 |
| | P= 0.096 | P= 0.054 | P= 0.204 | P= 0.1 | **P= 0.035** | P= 0.106 | P= 0.051 | **P= 0.032** | P= 0.056 | P= 0.075 | **P= 0.021** | **P= 0.03** | P= 0.059 |
| **C100, C0** | T= 0.785 | T= 1.332 | T= 1.063 | T= 1.282 | T= 1.705 | T= 1.666 | T= 2.281 | **T= 2.876** | T= 1.636 | T= 1.825 | T= 2.255 | T= 2.683 | T= 1.425 |
| | P= 0.572 | P= 0.172 | P= 0.372 | P= 0.248 | P= 0.203 | P= 0.139 | P= 0.05 | **P= 0.024** | P= 0.172 | P= 0.124 | P= 0.054 | P= 0.079 | P= 0.196 |
| **C50, C10** | T= 1.800 | **T= 2.095** | T= 1.050 | T= 1.176 | T= 1.671 | T= 1.516 | T= 1.773 | T= 1.900 | T= 1.957 | T= 1.584 | T= 1.250 | T= 1.814 | T= 1.495 |
| | P= 0.059 | **P= 0.025** | P= 0.453 | P= 0.259 | P= 0.092 | P= 0.154 | P= 0.088 | P= 0.061 | P= 0.099 | P= 0.162 | P= 0.267 | P= 0.08 | P= 0.206 |
| **C50, C0** | T= 0.939 | T= 1.631 | T= 1.151 | T= 0.782 | T= 0.984 | T= 1.408 | T= 1.89 | T= 2.192 | T= 1.494 | T= 1.438 | T= 1.627 | T= 1.056 | T= 0.675 |
| | P= 0.413 | P= 0.143 | P= 0.431 | P= 0.535 | P= 0.405 | P= 0.242 | P= 0.08 | P= 0.059 | P= 0.241 | P= 0.228 | P= 0.088 | P= 0.341 | P= 0.635 |
| **C10, C0** | T= 1.251 | T= 0.550 | T= 0.838 | T= 0.591 | T= 0.347 | T= 0.407 | T= 0.168 | T= 0.560 | T= 0.206 | T= 0.505 | T= 1.041 | T= 0.494 | T= 0.624 |
| | P= 0.22 | P= 0.759 | P= 0.497 | P= 0.778 | P= 0.902 | P= 0.846 | P= 0.943 | P= 0.719 | P= 0.849 | P= 0.749 | P= 0.325 | P= 0.767 | P= 0.595 |
| **Scarborough South** | | | | | | | | | | | | | |
| **C100, C50** | T= 1.368 | T= 1.639 | T= 1.850 | T= 2.113 | T= 2.155 | T= 1.923 | T= 2.361 | T= 2.424 | T= 2.182 | **T= 3.842** | T= 1.640 | T= 1.286 | T= 0.891 |
| | P= 0.216 | P= 0.119 | P= 0.112 | P= 0.068 | P= 0.081 | P= 0.084 | P= 0.058 | P= 0.064 | P= 0.071 | **P= 0.037** | P= 0.139 | P= 0.211 | P= 0.431 |
| **C100, C10** | T= 1.851 | T= 2.086 | T= 2.417 | **T= 4.288** | **T= 3.721** | **T= 3.590** | **T= 5.118** | **T= 4.514** | **T= 3.466** | **T= 3.467** | T= 2.538 | **T= 4.192** | T= 1.148 |
| | P= 0.093 | P= 0.075 | P= 0.065 | **P= 0.024** | **P= 0.025** | **P= 0.029** | **P= 0.028** | **P= 0.03** | **P= 0.028** | **P= 0.027** | P= 0.064 | **P= 0.027** | P= 0.277 |
| **C100, C0** | T= 0.547 | T= 0.844 | T= 1.241 | T= 1.453 | T= 1.283 | T= 1.256 | T= 1.574 | T= 1.240 | T= 1.028 | T= 1.041 | T= 1.102 | T= 1.352 | T= 1.161 |
| | P= 0.558 | P= 0.466 | P= 0.265 | P= 0.204 | P= 0.23 | P= 0.252 | P= 0.152 | P= 0.278 | P= 0.388 | P= 0.382 | P= 0.367 | P= 0.292 | P= 0.295 |
| **C50, C10** | T= 1.087 | T= 1.712 | T= 1.417 | T= 1.578 | **T= 2.138** | T= 1.594 | T= 1.767 | T= 1.174 | **T= 1.811** | T= 1.111 | T= 1.426 | **T= 2.246** | T= 0.508 |
| | P= 0.375 | P= 0.062 | P= 0.136 | P= 0.057 | **P= 0.033** | P= 0.063 | P= 0.114 | P= 0.363 | **P= 0.032** | P= 0.366 | P= 0.209 | **P= 0.031** | P= 0.826 |
| **C50, C0** | T= 1.100 | T= 1.321 | T= 0.896 | T= 0.430 | T= 0.945 | T= 0.701 | T=0.6747 | T= 1.034 | T= 1.787 | T= 1.308 | T= 1.163 | T= 0.680 | T= 1.170 |
| | P= 0.306 | P= 0.201 | P= 0.566 | P= 0.795 | P= 0.422 | P= 0.621 | P= 0.719 | P= 0.314 | P= 0.131 | P= 0.241 | P= 0.404 | P= 0.555 | P= 0.337 |
| **C10, C0** | T= 1.561 | T= 1.371 | T= 0.946 | T= 1.461 | T= 1.923 | T= 1.733 | T= 1.690 | T= 1.918 | **T= 3.042** | T= 1.335 | T= 1.313 | T= 2.090 | T= 0.708 |
| | P= 0.247 | P= 0.187 | P= 0.409 | P= 0.175 | P= 0.073 | P= 0.052 | P= 0.094 | P= 0.141 | **P= 0.029** | P= 0.254 | P= 0.348 | P= 0.106 | P= 0.58 |

In the MDS plot for Scarborough North (Fig. 4.2A), community composition of C100 closely resembled that of C50 and they were tightly clustered together, irrespective of the season, while C0 and C10 were more variable and scattered among the seasons. At Scarborough South (Fig. 4.2B), community compositions of C100 were also most similar to those of C50, while C10 and C0 overlapped substantially. A second emergent pattern at both sites was that seasonal differences (as evident in the spread of data) were more pronounced in the C0 and C10 treatments than for C50 and C100.

The clusters evident in the MDS were underpinned by particular functional groups that were prominent at different density levels (Fig. 4.2C, D). Bare rock was positively associated with higher limpet density treatments (C50 and C100), whereas most algal groups, mussels, other filter feeders and whelks were positively associated with lower density treatments (C0 and C10). Strongest predictors were bare rock, and corticated, ephemeral and crustose algae.

The community composition displayed a seasonal cycle that was evident in temporal trajectories. The community composition changed over time until about T10 in September, when it returned to a state similar to that observed at the beginning of the observations, and then began a repeat trajectory (Fig. 4.3A, B). Another pattern was that the trajectories for Scarborough North grouped together the C100 and C50 densities, distinct from those of C10 and C0; whereas at Scarborough South the four trajectories were non-overlapping, with that for C100 most closely aligned with C0, and C50 with C10.

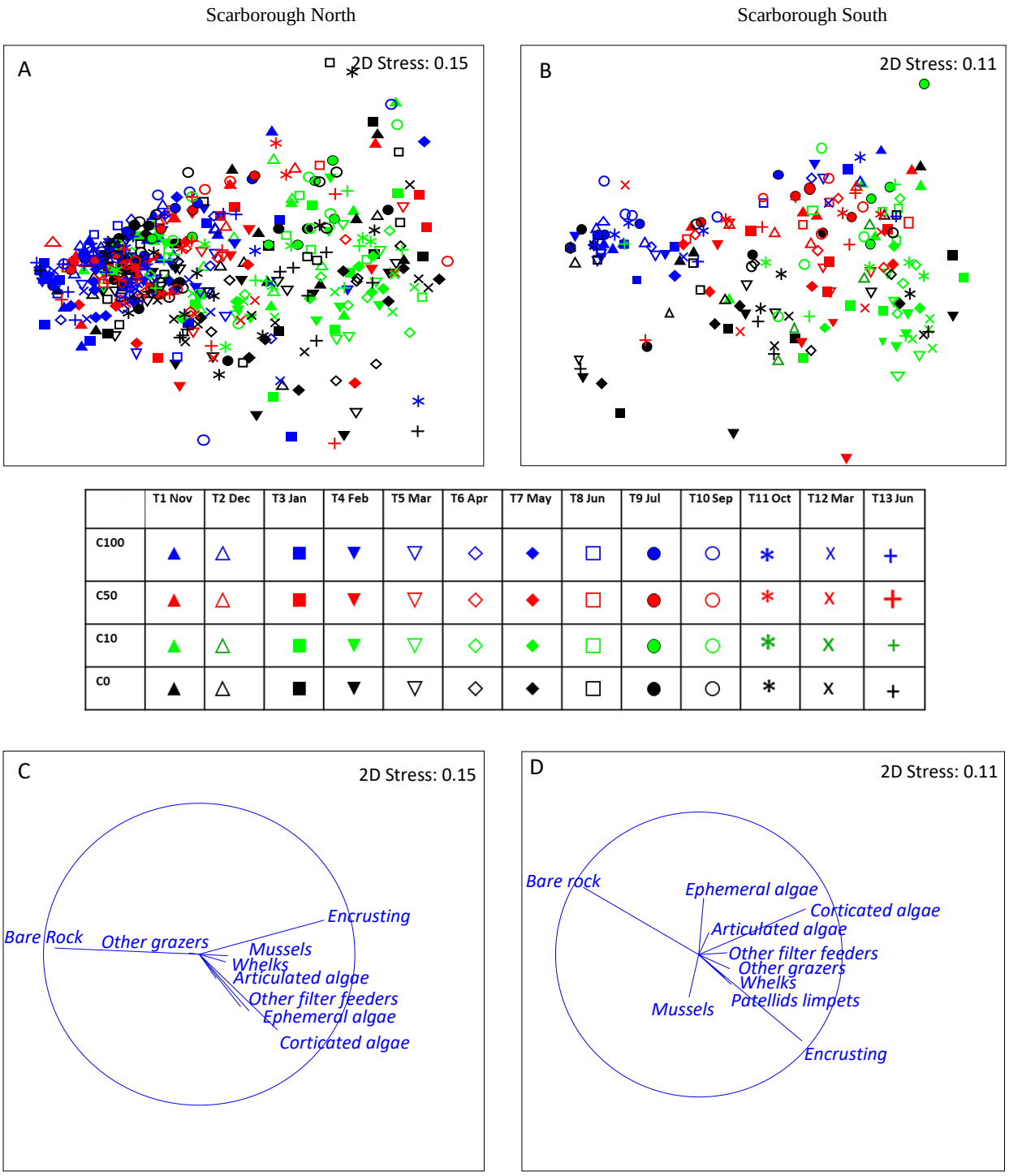



Figure 4.2. Multidimensional Scaling (A, B) and associated vectors of based on correlations with percentage cover of functional groups (C, D) under different densities of *C. granatina* in exclusion cages, at (A, C) Scarborough North, and (B, D) Scarborough South. C100 = 100% density (blue symbols); C50 = 50% density (red symbols); C10 = 10% density (green symbols); C0 = 0% density (black symbols). Different shapes reflect time in months from T1 to T13.

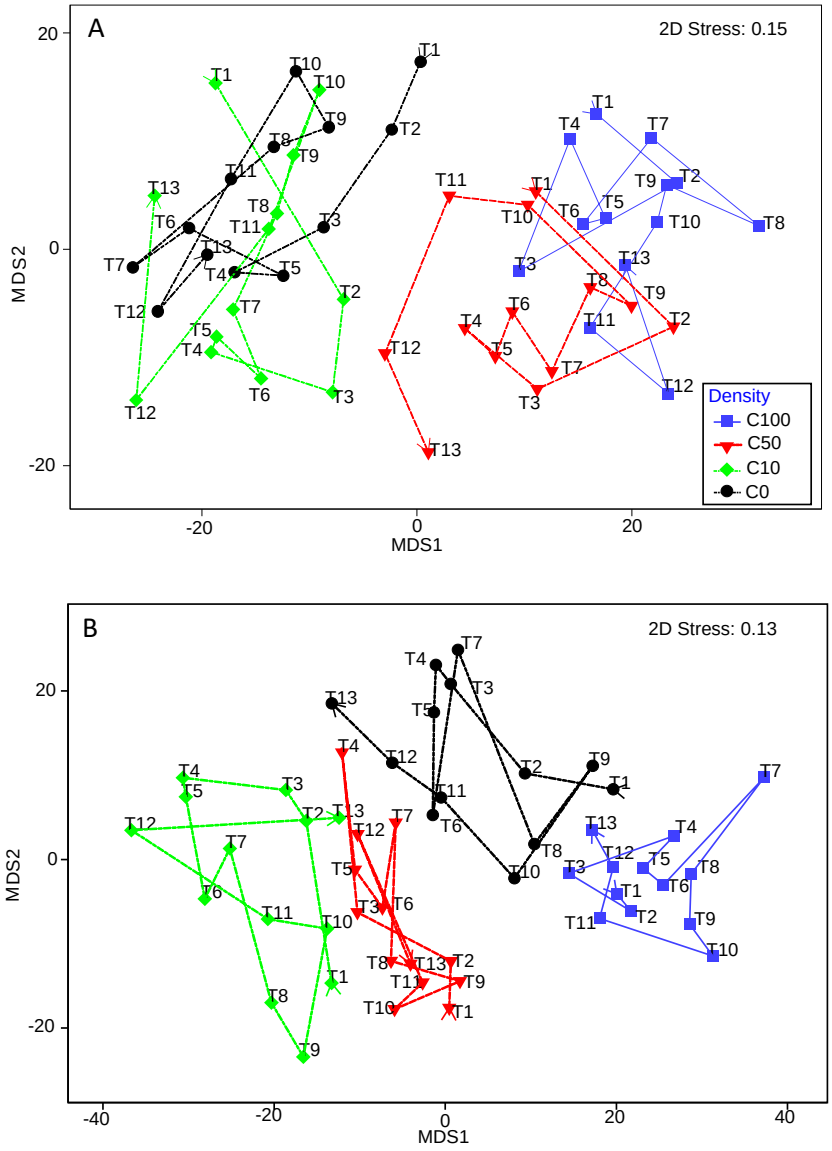



Figure 4.3. MDS temporal trajectories for the two sites (A = Scarborough North; B = Scarborough South) based on the percentage cover of functional groups under different limpet densities. T1 to T13 indicate time in months when samples were collected; for further explanation see keys in Fig. 4.2.

SIMPER identified the functional groups responsible for differences between community composition of C100 (i.e. under natural densities) and other (i.e. reduced) limpet densities (C50, C10 and C0) (Table 4.6; and see Fig. 4.4 for a summary of mean values illustrating trends among limpet densities).

At Scarborough North (Table 4.6A, Fig. 4.4), C100 had the highest cover of bare rock and C0 and C10 the lowest cover. Conversely, C0 and C10 had highest cover of corticated, ephemeral and encrusting algae, and C100 lowest values. Other filter feeders were most abundant in C50 and C10, frequently least abundant in C100 and, unexpectedly, also in C0. Thus, other filter feeders reached greatest cover at intermediate limpet densities. Surprisingly, C0 had high bare rock and low algae. Bare rock, corticated and encrusting algae were the main drivers of the differences in community compositions between reduced limpet densities and natural densities throughout the study, while contribution of ephemeral algae appeared to be seasonally focussed between February and May (Table 4.7A). Other filter feeders mostly contributed to differences in community composition between C50 and C100; their contribution to differences between C10 and C100 was less frequent.

At Scarborough South (Table 4.6B, Fig. 4.4), C100 again had the highest bare rock throughout time, while corticated algae and ephemeral algae increased in low-density plots and became the determining functional groups for C10 and C0, and were always least abundant in (and often absent from) C100. Encrusting algae were most prevalent in C50 and C10, always least abundant in C100, and also had low cover in C0. Other filter feeders were least abundant in C100 and rose as limpet density dropped, except for a decline in C0; but the differences among limpet densities were not significant. Bare rock, corticated algae and encrusting algae again were the main contributors to the differences in community compositions between the natural limpet densities (C100) and density manipulations (Table 4.7B). Ephemeral algae and whelks occasionally contributed to differences between C100 and C0.

**Table 4.6A**. Scarborough North: Percentage cover of functional groups identified by SIMPER as most influential in distinguishing communities between different limpet density manipulations over time (November 2017 to June 2019). C100 = 100% density; C50 = 50% density; C10 = 10% density; C0 = 0% density. The data have been standardised and square-root transformed).

| Functional groups | Density | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Corticated** | **C100** | 0.00 | 0.00 | 1.00 | 0.59 | 0.53 | 0.79 | 0.00 | 0.00 | 0.00 | 0.00 | 1.11 | 1.09 | 0.26 |
| | **C50** | 0.35 | 0.27 | 1.70 | 1.88 | 1.80 | 1.35 | 1.46 | 0.60 | 0.00 | 0.58 | 1.62 | 3.48 | 2.21 |
| | **C10** | 2.46 | 2.87 | 2.47 | 3.73 | 4.43 | 4.59 | 4.43 | 2.25 | 2.13 | 0.91 | 3.40 | 6.27 | 4.43 |
| | **C0** | 1.39 | 2.03 | 2.97 | 3.64 | 3.47 | 3.75 | 4.48 | 2.81 | 1.54 | 1.05 | 3.02 | 5.28 | 4.18 |
| **Ephemeral** | **C100** | 0.00 | 0.00 | 0.23 | 0.54 | 0.23 | 1.22 | 0.79 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | **C50** | 0.60 | 0.00 | 0.82 | 1.97 | 1.41 | 1.95 | 0.81 | 0.25 | 0.24 | 0.65 | 0.44 | 0.37 | 0.44 |
| | **C10** | 1.21 | 0.40 | 1.82 | 2.48 | 2.40 | 1.98 | 1.31 | 1.97 | 0.99 | 1.41 | 1.70 | 0.97 | 0.44 |
| | **C0** | 0.00 | 0.33 | 0.45 | 1.28 | 1.69 | 2.40 | 2.10 | 0.70 | 0.99 | 0.94 | 0.45 | 0.17 | 0.58 |
| **Encrusting** | **C100** | 3.25 | 3.03 | 2.76 | 3.17 | 2.59 | 2.29 | 2.49 | 2.00 | 3.07 | 2.98 | 2.47 | 1.03 | 2.43 |
| | **C50** | 3.23 | 1.57 | 1.86 | 2.64 | 2.49 | 2.93 | 1.84 | 2.47 | 2.99 | 3.32 | 4.04 | 3.17 | 2.94 |
| | **C10** | 6.84 | 5.17 | 3.71 | 4.96 | 4.80 | 4.51 | 5.32 | 5.77 | 6.34 | 6.93 | 5.34 | 5.13 | 6.13 |
| | **C0** | 4.57 | 4.44 | 4.85 | 4.39 | 4.51 | 5.20 | 4.93 | 6.52 | 6.34 | 6.80 | 7.05 | 5.04 | 4.68 |
| **Bare rock** | **C100** | 8.30 | 9.28 | 8.80 | 9.00 | 9.29 | 9.16 | 9.20 | 9.57 | 9.25 | 9.10 | 9.24 | 9.69 | 9.05 |
| | **C50** | 8.63 | 9.61 | 9.02 | 8.47 | 8.87 | 8.80 | 9.04 | 9.23 | 9.03 | 8.81 | 8.12 | 7.82 | 8.18 |
| | **C10** | 3.62 | 7.05 | 6.89 | 5.71 | 5.72 | 4.98 | 5.68 | 6.26 | 6.30 | 5.10 | 6.33 | 3.90 | 4.77 |
| | **C0** | 6.79 | 7.28 | 6.79 | 6.43 | 6.44 | 5.28 | 5.22 | 5.53 | 5.93 | 5.98 | 3.68 | 4.17 | 6.17 |
| **Other filter feeders** | **C100** | 0.78 | 0.26 | 1.57 | 0.00 | 0.49 | 0.35 | 0.00 | 0.00 | 0.50 | 0.89 | 0.26 | 0.24 | 0.75 |
| | **C50** | 1.84 | 0.96 | 1.92 | 1.68 | 1.54 | 1.00 | 1.14 | 1.22 | 1.56 | 1.50 | 0.43 | 1.24 | 1.22 |
| | **C10** | 1.72 | 1.83 | 2.24 | 1.87 | 0.57 | 1.91 | 1.04 | 0.70 | 0.84 | 1.12 | 0.72 | 0.52 | 0.42 |
| | **C0** | 0.35 | 0.25 | 0.46 | 0.40 | 0.92 | 0.41 | 0.00 | 0.79 | 0.84 | 0.23 | 0.41 | 0.51 | 0.59 |

**Table 4.6B**. Scarborough South: Percentage cover of functional groups identified by SIMPER as most influential in distinguishing communities between different limpet densities over time (November 2017 to June 2019). C = caged. 100 = control density of *C. granatina* of 100%; 50 = density reduced to 50%; 10 = density reduced to 10%; 0 = zero density. The data have been standardised and square-root transformed).

| Functional groups | Density | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Corticated** | **C100** | 0.25 | 0.27 | 0.43 | 0.00 | 0.00 | 0.00 | 0.32 | 0.00 | 0.00 | 0.00 | 0.00 | 0.61 | 0.97 |
| | **C50** | 0.84 | 1.20 | 2.96 | 5.20 | 3.07 | 1.95 | 2.29 | 1.27 | 0.52 | 1.06 | 1.07 | 3.68 | 1.98 |
| | **C10** | 2.60 | 5.17 | 5.83 | 6.59 | 6.22 | 4.39 | 5.28 | 2.00 | 1.61 | 2.81 | 3.99 | 6.74 | 3.38 |
| | **C0** | 0.75 | 2.10 | 3.57 | 4.32 | 3.03 | 3.10 | 3.26 | 1.18 | 1.79 | 1.39 | 3.52 | 4.61 | 4.60 |
| **Ephemeral** | **C100** | 0.00 | 0.00 | 0.59 | 0.51 | 0.75 | 0.25 | 0.65 | 0.25 | 0.00 | 1.39 | 0.00 | 0.00 | 0.00 |
| | **C50** | 0.00 | 0.00 | 0.22 | 1.41 | 0.92 | 0.63 | 1.51 | 0.50 | 0.00 | 0.00 | 0.00 | 0.53 | 0.56 |
| | **C10** | 0.00 | 0.00 | 1.15 | 1.59 | 1.44 | 0.85 | 1.32 | 2.08 | 0.00 | 0.56 | 0.00 | 0.62 | 1.94 |
| | **C0** | 0.00 | 0.00 | 2.45 | 2.46 | 1.45 | 1.25 | 2.24 | 1.03 | 0.00 | 0.00 | 0.00 | 0.00 | 1.94 |
| **Encrusting** | **C100** | 3.53 | 3.56 | 3.79 | 3.39 | 3.53 | 3.29 | 1.83 | 2.84 | 2.77 | 2.09 | 4.43 | 3.17 | 3.91 |
| | **C50** | 7.69 | 7.41 | 7.44 | 4.29 | 6.86 | 7.19 | 5.87 | 7.34 | 7.31 | 7.98 | 7.79 | 4.62 | 6.11 |
| | **C10** | 7.70 | 5.96 | 6.61 | 6.81 | 6.95 | 8.17 | 7.28 | 8.64 | 8.80 | 6.64 | 7.69 | 7.00 | 6.09 |
| | **C0** | 4.58 | 3.83 | 4.40 | 3.10 | 4.28 | 5.02 | 4.17 | 4.47 | 3.20 | 4.65 | 4.71 | 4.33 | 3.89 |
| **Bare rock** | **C100** | 7.93 | 8.15 | 8.07 | 8.39 | 8.43 | 8.62 | 9.65 | 9.05 | 8.79 | 9.19 | 7.80 | 8.49 | 7.78 |
| | **C50** | 5.43 | 6.07 | 5.22 | 5.53 | 5.55 | 5.59 | 6.46 | 5.46 | 5.94 | 5.05 | 5.35 | 6.17 | 6.02 |
| | **C10** | 4.36 | 5.04 | 3.17 | 1.99 | 1.92 | 2.23 | 3.05 | 3.32 | 2.42 | 5.25 | 3.78 | 0.97 | 4.82 |
| | **C0** | 7.34 | 7.59 | 5.30 | 5.48 | 6.62 | 6.41 | 6.46 | 7.35 | 7.91 | 7.24 | 6.48 | 5.90 | 5.67 |
| **Whelks** | **C100** | 0.00 | 0.27 | 0.78 | 0.00 | 0.26 | 0.53 | 0.00 | 0.43 | 1.87 | 2.33 | 0.96 | 0.62 | 0.37 |
| | **C50** | 0.00 | 0.24 | 0.33 | 1.11 | 1.16 | 0.94 | 0.00 | 1.57 | 2.01 | 2.31 | 1.25 | 1.43 | 1.13 |
| | **C10** | 0.00 | 0.72 | 0.62 | 0.87 | 1.21 | 1.12 | 0.80 | 1.23 | 0.75 | 3.33 | 0.94 | 1.21 | 0.65 |
| | **C0** | 0.00 | 0.41 | 0.77 | 0.00 | 1.57 | 0.66 | 0.00 | 1.53 | 2.72 | 1.72 | 0.54 | 0.60 | 0.00 |

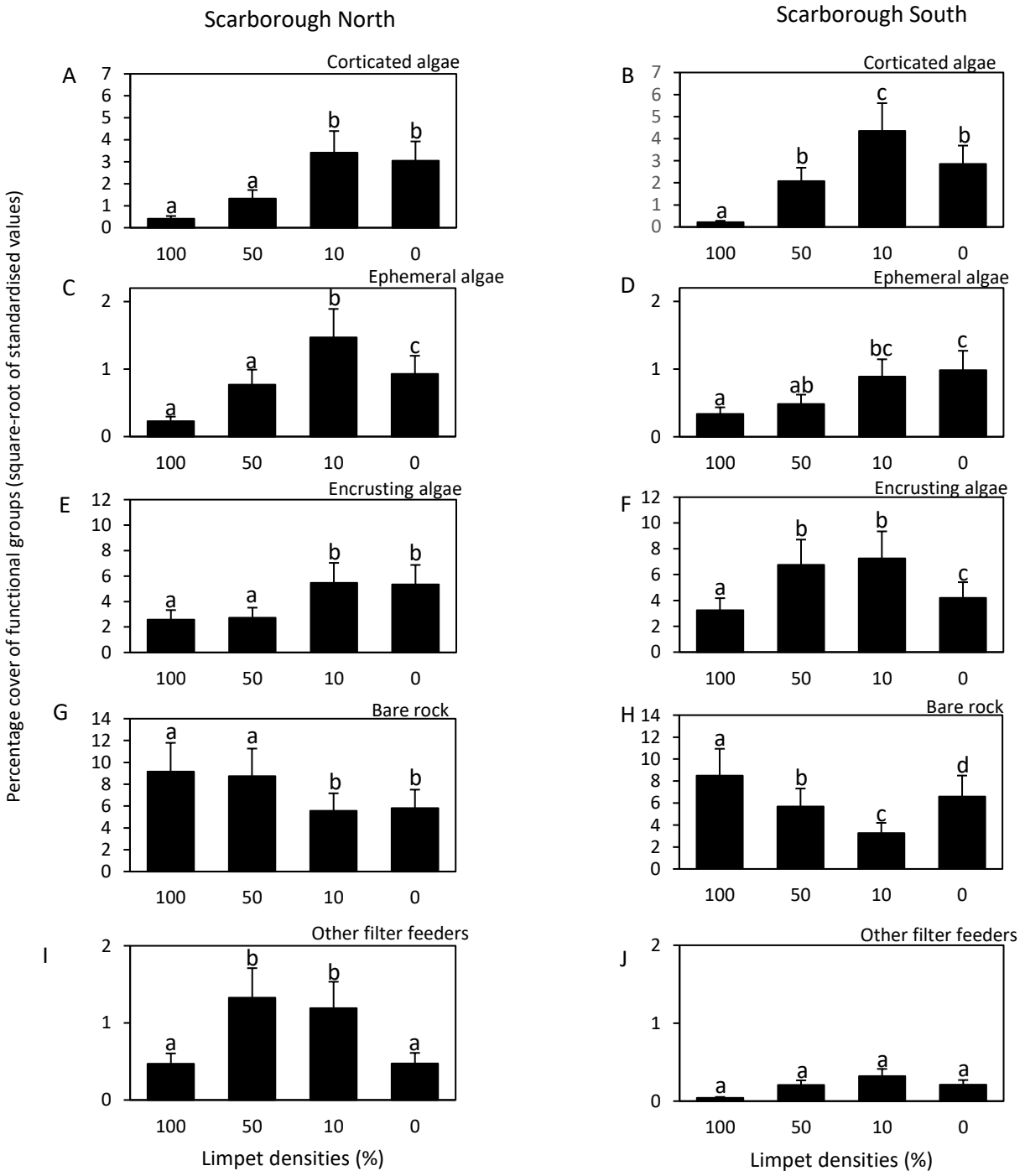



Figure 4.4: Mean (+1SE) percentage cover of functional groups that contributed >10% to differences between plots at different limpet densities at both Scarborough North and Scarborough South. Limpet densities: 100 = control densities, 50 = 50% reduction, 10 = reduction to 10%, 0 = removal of all limpets. Different letters on top of the bars indicate significant differences.

**Table 4.7A**. Percentage contribution of functional groups to the differences in community composition between different limpet density manipulations and natural densities (C100) over time (November 2017 to June 2019) at Scarborough North. C100 = 100% density; C50 = 50% density; C10 = 10% density; C0 = 0% density. (The data have been standardised and square-root transformed.) Blank cells indicate times when SIMPER did not show any significant contribution to the differences. Rows for C100 remain blank because all comparisons are between C100 and other densities.

| Functional groups | Density | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Corticated** | **C100** | | | | | | | | | | | | | |
| | **C50** | | | 17.6 | 15.3 | 18.1 | 14.1 | 17.1 | 8.1 | | 7.5 | 13.1 | 29.7 | 18.9 |
| | **C10** | 11.9 | 25.1 | 16.2 | 22.3 | 25.8 | 24.4 | 29.2 | 15.2 | 16.0 | 6.1 | 16.0 | 28..0 | 25.1 |
| | **C0** | 12.4 | 21.7 | 20.4 | 25.7 | 23.2 | 20.1 | 30.1 | 18.2 | 13.3 | 8.3 | 14.2 | 28.7 | 27.0 |
| **Ephemeral** | **C100** | | | | | | | | | | | | | |
| | **C50** | 6.8 | | 9.2 | 16.7 | 13.8 | 19.7 | 11.1 | | | 8.5 | | | |
| | **C10** | 6.6 | | 12.4 | 13.9 | 14.3 | 11.2 | 8.1 | 13.6 | 7.2 | 9.2 | 11.5 | 5.0 | |
| | **C0** | | | 3.9 | 10.5 | 12.0 | 12.6 | 11.6 | 4.5 | | 7.4 | | | 3.8 |
| **Encrusting** | **C100** | | | | | | | | | | | | | |
| | **C50** | 38.4 | 33.3 | 23.8 | 23.2 | 20.7 | 25.2 | 26.4 | 24.4 | 30.3 | 29.0 | 30.6 | 23.9 | 26.4 |
| | **C10** | 27.8 | 22.2 | 22.8 | 18.5 | 18.6 | 17.7 | 24.1 | 26.7 | 27.5 | 30.8 | 23.1 | 21.9 | 26.6 |
| | **C0** | 40.5 | 34.8 | 28.8 | 25.1 | 22.6 | 23.8 | 22.7 | 30.8 | 34.1 | 35.6 | 29.2 | 25.0 | 26.6 |
| **Bare rock** | **C100** | | | | | | | | | | | | | |
| | **C50** | 21.4 | 7.3 | 11.0 | 10.6 | 8.3 | 9.4 | 9.5 | 8.4 | 13.8 | 15.0 | 17.9 | 18.9 | 13.6 |
| | **C10** | 30.3 | 18.7 | 17.7 | 22.8 | 23.4 | 26.7 | 24.0 | 22.7 | 23.1 | 30.0 | 20.3 | 30.2 | 27.6 |
| | **C0** | 32.2 | 26.1 | 24.3 | 26.8 | 23.7 | 26.1 | 28.6 | 26.7 | 31.9 | 28.0 | 32.9 | 33.3 | 22.9 |
| **Other** | **C100** | | | | | | | | | | | | | |
| **filter** | **C50** | 15.4 | 17.5 | 20.6 | 15.9 | 14.3 | 12.4 | 13.0 | 17.2 | 21.0 | 17.4 | 6.7 | 12.2 | 9.6 |
| **feeders** | **C10** | 8.6 | 14.0 | 14.5 | 12.3 | 5.2 | 10.4 | 6.7 | 4.6 | 6.3 | 8.9 | 5.9 | 3.23 | 4.5 |
| | **C0** | 7.2 | 4.0 | 12.5 | 3.0 | 7.7 | 3.8 | | 5.0 | 5.4 | 7.4 | 3.2 | | 6.0 |

**Table 4.7B**. Percentage contribution of functional groups to the differences in community composition between different limpet density manipulations and natural densities (C100) over time (November 2017 to June 2019) at Scarborough South. C100 = 100% density; C50 = 50% density; C10 = 10% density; C0 = 0% density. (The data have been standardised and square-root transformed.) Blank cells indicate times when SIMPER did not show any significant contribution to the differences. Rows for C100 remain blank because all comparisons are between C100 and other densities.

| Functional groups | Density | T1 Nov | T2 Dec | T3 Jan | T4 Feb | T5 Mar | T6 Apr | T7 May | T8 Jun | T9 Jul | T10 Sep | T11 Oct | T12 Mar | T13 Jun |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Corticated** | **C100** | | | | | | | | | | | | | |
| | **C50** | 6.00 | 9.1 | 18.8 | 28.0 | 21.9 | 14.8 | 15.8 | 9.2 | | 7.8 | 9.4 | 22.2 | 10.9 |
| | **C10** | 15.6 | 31.3 | 32.6 | 34.3 | 33.6 | 23.7 | 25.8 | 10.9 | 8.4 | 15.7 | 26.6 | 32.5 | 27.6 |
| | **C0** | 6.5 | 17.6 | 21.0 | | 20.4 | 22.5 | 26.8 | 11.5 | 18.0 | 13.9 | 28.0 | 34.8 | 31.2 |
| **Ephemeral** | **C100** | | | | | | | | | | | | | |
| | **C50** | | | | 6.2 | | 4.9 | 9.6 | | | | | | |
| | **C10** | | | 5.9 | 5.9 | 4.4 | 4.3 | 5.3 | 10.0 | | 3.4 | | | |
| | **C0** | | | 17.7 | 16.3 | 14.9 | 7.9 | 21.3 | 9.0 | | | | | 9.4 |
| **Encrusting** | **C100** | | | | | | | | | | | | | |
| | **C50** | 43.2 | 39.9 | 32.9 | 20.1 | 30.5 | 36.6 | 31.3 | 37.1 | 44.4 | 45.1 | 37.3 | 28.7 | 40.1 |
| | **C10** | 34.4 | 24.0 | 24.0 | 23.5 | 23.9 | 29.5 | 29.5 | 33.1 | 32.8 | 27.3 | 28.0 | 25.4 | 33.7 |
| | **C0** | 44.1 | 33.1 | 23.2 | | 24.5 | 28.3 | 25.5 | 33.5 | 35.4 | 39.4 | 30.4 | 27.3 | 26.9 |
| **Whelks** | **C100** | | | | | | | | | | | | | |
| | **C50** | | | 5.7 | 5.9 | 6.8 | 5.4 | | 10.3 | 13.7 | 4.2 | 7.0 | 6.7 | 7.2 |
| | **C10** | | 4.6 | 4.7 | 4.3 | 5.9 | 5.7 | 3.8 | 6.1 | 9.8 | | | 5.0 | 5.8 |
| | **C0** | | 4.5 | 5.5 | | 10.2 | 5.7 | | 14.8 | 20.3 | 12.5 | 8.6 | 7.1 | |
| **Bare rock** | **C100** | | | | | | | | | | | | | |
| | **C50** | 36.1 | 29.3 | 24.8 | 23.2 | 21.7 | 24.8 | 27.0 | 26.0 | 28.8 | 30.5 | 29.9 | 23.4 | 35.0 |
| | **C10** | 30.7 | 25.5 | 24.3 | 25.6 | 25.1 | 29.9 | 26.0 | 28.9 | 34.9 | 37.1 | 27.1 | 26.8 | 25.2 |
| | **C0** | 34.9 | 22.9 | 20.9 | | 16.6 | 28.7 | 17.6 | 24.1 | 23.4 | 23.1 | 23.8 | 21.6 | 28.3 |

*Effects of limpet thinning on key functional groups*

Many of the functional groups were insufficiently abundant to meaningfully trace changes in abundance relative to limpet densities over time, so I concentrated on patterns emerging in corticate, ephemeral and crustose algae, grazers, whelks and the recruits of *C. granatina*, which displayed significant effects.

*Percentage cover of algae*

Three-way Repeated Measures ANOVAs (Table 4.8) on the percentage cover of corticated algae indicated that their abundances were significantly influenced by significant interactions between density and time, and between site and density. Thus, the effects of limpet removals (density) on corticated algae depended on the time and site. This is reflected in the effects of limpet density only being detectable on the C10 and C0 during the season when the abundance of algae rose (Fig. 4.5). For ephemeral algae, a significant main effect of time and an interaction between site and density emerged. The effects of limpet removals on ephemeral algae were thus site-dependent, reflecting a steady increase with decreasing limpet densities at Scarborough South, while maximum cover of ephemeral algae occurred at 10% limpet densities at Scarborough North (Fig. 4.4).

At both sites, corticated algae attained highest percentage cover in the two lowest-density plots, C10 and C0 (Fig. 4.5A, B; Fig. 4.4A, B). In both years, percentage cover showed a clear seasonal pattern in the C0 and C10 plots, and to a lesser extent also in C50; but none in C100, where abundance was consistently low or even zero. Ephemeral algae (Fig. 4.5C, D) were also more abundant in C10 and C0 (most obviously in the first year) and showed a seasonal pattern, reaching greater cover in the summer upwelling season (January to May) in the first year, but declining to low percentage cover over the remainder of the period.

There was also a significant interaction between site and density on the percentage cover of encrusting algae, because their abundance was greatest under low limpet densities at Scarborough North and under intermediate densities at Scarborough South (Table 4.8, Fig.

4.5E, F, Fig. 4.4E, F). Interestingly, percentage cover of algal crusts did not change significantly among seasons.

**Table 4.8**. Results of three-way Repeated Measures ANOVAs on caged treatments, testing for the effects of site, limpet density and time on the percentage cover of corticated, ephemeral and encrusting algae. Asterisks indicate significant effects. Data were square-root transformed for analysis.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| **Corticated algae** | | | | | |
| Site | 1 | 568 | 568 | 2.220 | 0.137 |
| Density | 3 | 58397 | 19466 | 10.910 | <0.001* |
| Time | 12 | 51888 | 4324 | 16.906 | <0.001* |
| Site: Density | 3 | 2518 | 839 | 3.281 | 0.021* |
| Site: Time | 12 | 4130 | 344 | 1.346 | 0.192 |
| Density: Time | 36 | 35609 | 989 | 3.867 | <0.001* |
| Site: Density: Time | 36 | 5955 | 165 | 0.647 | 0.943 |
| Residuals | 300 | 76731 | 256 | | |
| **Ephemeral algae** | | | | | |
| Site | 1 | 0 | 0.02 | 0.000 | 0.984 |
| Density | 3 | 1174 | 391.5 | 2.414 | 0.117 |
| Time | 12 | 1687 | 140.60 | 2.626 | <0.002* |
| Site: Density | 3 | 554 | 184.76 | 3.450 | 0.017* |
| Site: Time | 12 | 641 | 53.42 | 0.997 | 0.451 |
| Density: Time | 36 | 1831 | 50.87 | 0.950 | 0.555 |
| Site: Density: Time | 36 | 1420 | 39.45 | 0.737 | 0.866 |
| Residuals | 300 | 16066 | 53.55 | | |
| **Encrusting algae** | | | | | |
| Site | 1 | 29988 | 29988 | 76.395 | <0.001* |
| Density | 3 | 94892 | 31631 | 2.31 | 0.128 |
| Time | 12 | 5954 | 496 | 1.264 | 0.239 |
| Site: Density | 3 | 48318 | 16106 | 41.030 | <0.001* |
| Site: Time | 12 | 4926 | 411 | 1.046 | 0.407 |
| Density: Time | 36 | 15093 | 419 | 1.068 | 0.370 |
| Site: Density: Time | 36 | 12367 | 344 | 0.875 | 0.677 |
| Residuals | 300 | 117762 | 393 | | |

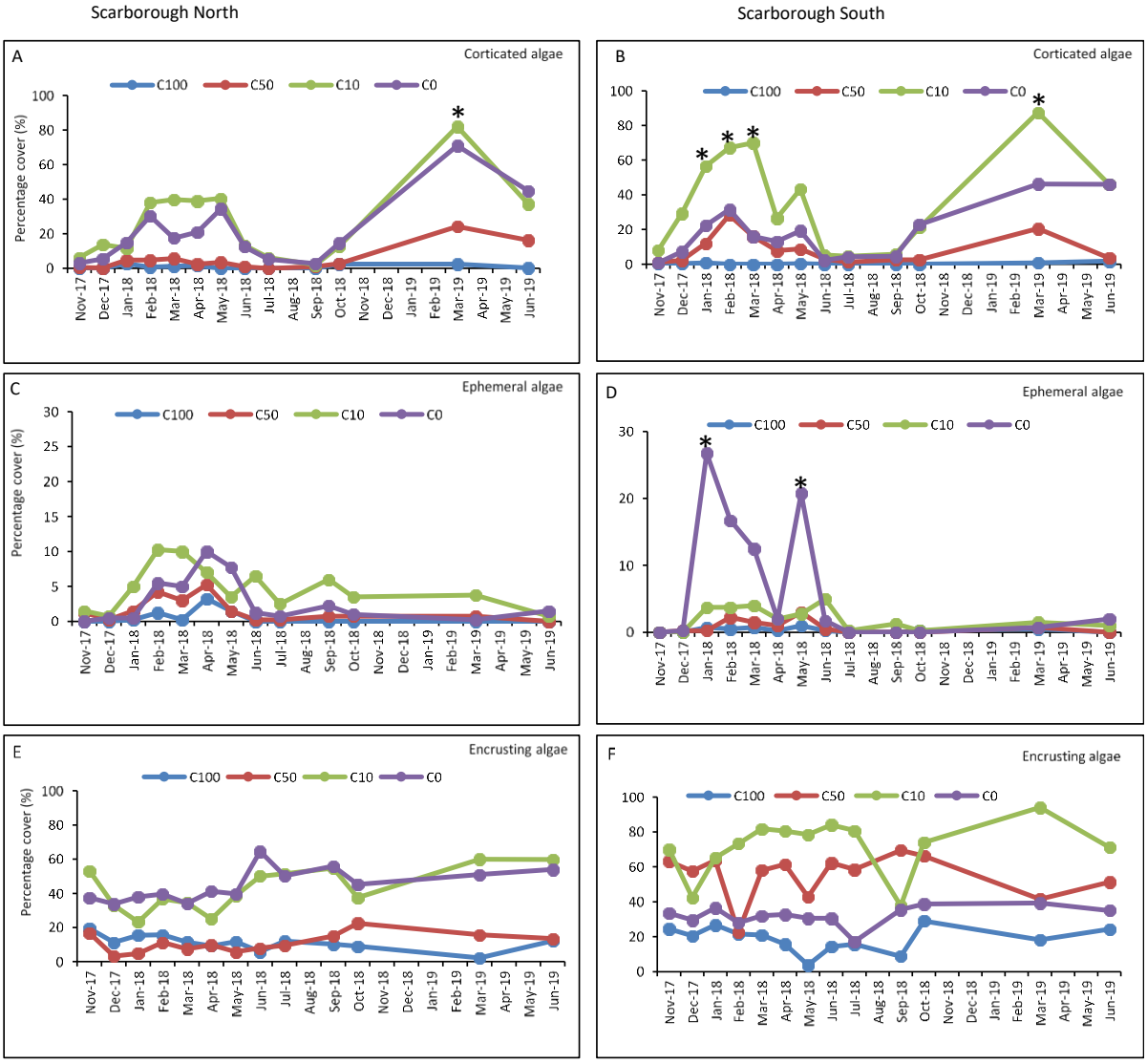



Figure 4.5. Differences in mean percentage cover of three functional groups of algae with regard to limpet density levels over time, at Scarborough North (left) and Scarborough South (right). The data are not standardised or transformed. Note differences in scale among functional groups. C100, C50, C10 and C0 respectively represent densities of *C. granatina* in caged plots of 100% (no reduction) and reductions to levels of 50%, 10% and zero. Instances where pairwise posthoc comparisons confirmed a significant effect of adult densities are indicated by asterisks.

*Effects of limpet thinning on other grazers*

The responses of other grazers (excluding *C. granatina* itself) to the thinning of *C. granatina* depended on an interactive effects between site and time (Table 4.9). At Scarborough North, abundance of grazers never changed over time and showed no obvious relationship with limpet densities. At Scarborough South, their abundance was markedly greater in C50 than in other plots from December 2017 until April 2018 (with the difference being significant in December 2017 and March 2018), before declining until the end of the experiment (Fig. 4.6). Interestingly, in Scarborough South, grazers appeared for only three months in C0 and disappeared thereafter (Fig. 4.6). As significant differences were evident at only one site, and then only twice in a single density-treatment, and the abundance of grazers was always low, the parsimonious interpretation is that density of *C. granatina* had no effect on other grazers.

**Table 4.9**. Results of three-way Repeated Measures ANOVA on the effects of site, limpet density and time on the abundance of grazers. Asterisks indicate significant effects. Data were square-root transformed for analysis.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| Site | 1 | 0.00 | 0.0024 | 0.003 | 0.960 |
| Density | 3 | 11.99 | 3.996 | 1.657 | 0.229 |
| Time | 12 | 29.40 | 2.4503 | 2.554 | 0.003* |
| Site: Density | 3 | 1.68 | 0.5601 | 0.584 | 0.626 |
| Site: Time | 12 | 36.90 | 3.0753 | 3.205 | <0.001* |
| Density: Time | 36 | 21.48 | 0.5967 | 0.622 | 0.957 |
| Site: Density: Time | 36 | 28.29 | 0.7858 | 0.819 | 0.762 |
| Residuals | 300 | 287.82 | 0.9594 | | |

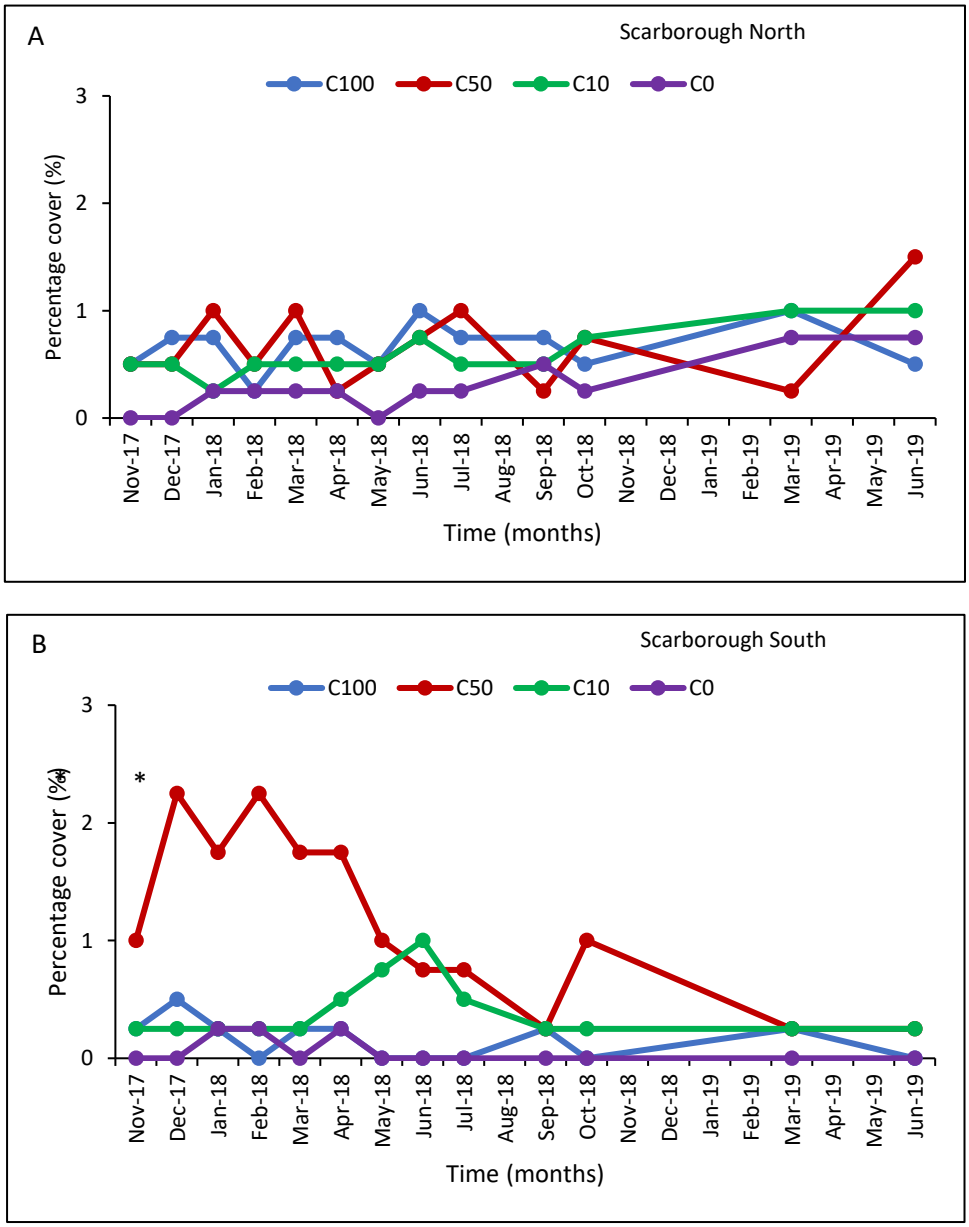


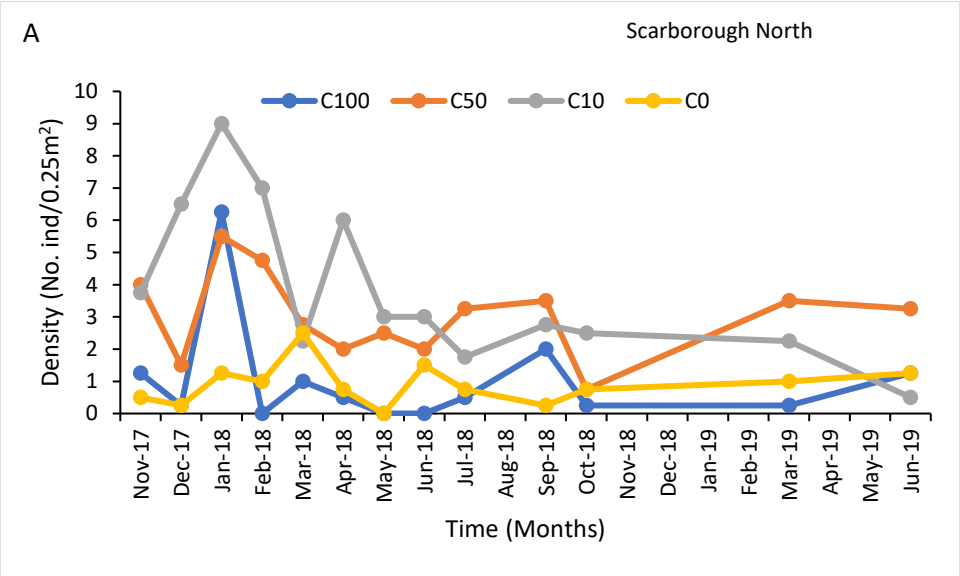

Figure 4.6. Differences in mean percentage cover of other grazers over time, in relation to limpet densities at two sites. See caption for Fig.4.5 for further details.

*Effects of limpet thinning on other filter feeders*

There was a significant main effect of time and an interaction of site and density on the percentage cover of other filter feeders, reflecting the fact that at both sites, percentage cover of other filter feeders was high in summer and autumn before declining and disappearing at Scarborough South (Table 4.10). At Scarborough North, thinning of *C. granatina* led to higher percentage cover of filter feeders in the C50 and C10 plots (Fig. 4.7A, Fig. 4.4I), whereas these differences did not occur at Scarborough South (Fig.4.7B, Fig. 4.4J).

**Table 4.10**. Results of a three-way Repeated Measures ANOVA on caged treatments, testing for the effects of site, limpet density and time (as well as their interactions) on the percentage cover of other filter feeders. Asterisks indicate significant effects. Data square-root transformed for analysis.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| Site | 1 | 286.1 | 286.12 | 36.880 | <0.001* |
| Density | 3 | 260.8 | 86.93 | 1.378 | 0.297 |
| Time | 12 | 198.1 | 16.51 | 2.128 | 0.015* |
| Site: Density | 3 | 100.4 | 33.46 | 4.313 | 0.005* |
| Site: Time | 12 | 120.4 | 10.03 | 1.293 | 0.222 |
| Density: Time | 36 | 194.5 | 5.40 | 0.696 | 0.906 |
| Site: Density: Time | 36 | 177.3 | 4.92 | 0.635 | 0.995 |
| Residuals | 300 | 2327.4 | 7.76 | | |



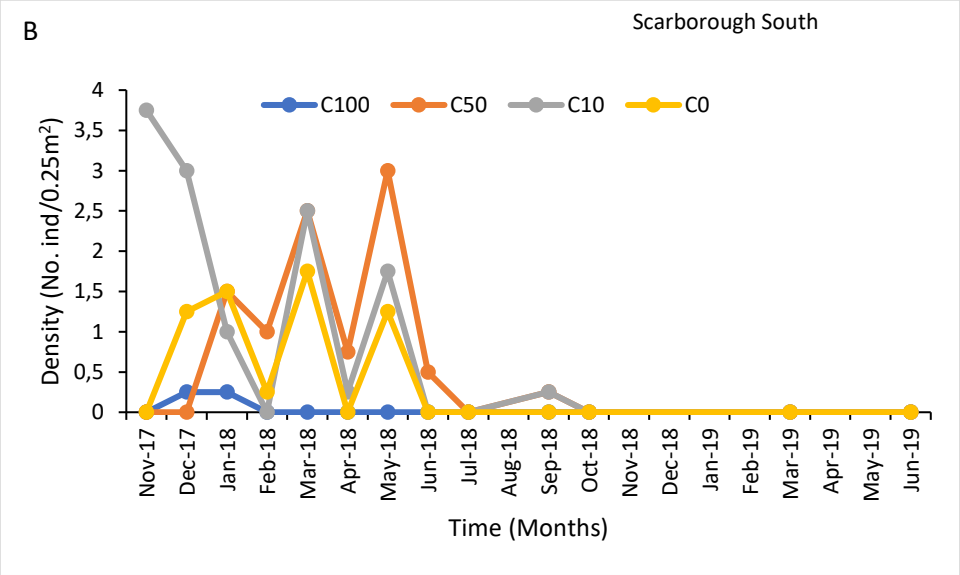




Figure 4.7. Differences in mean percentage cover of other filter feeders over time, in relation to limpet densities at two sites. See caption for Fig.4.5 for further details.

*The impact of thinning C. granatina density on percentage cover of bare rock*

There was a significant interaction of site and density on the amount of bare rock because the removal *C. granatina* had different effects on the prevalence of bare rock between sites (Table 4.11). At Scarborough North, bare rock was markedly higher in plots with high densities of limpets (C100 and C50), as might be expected (Fig. 4.4G), whereas at Scarborough South it was highest in C100 and, surprisingly, in C0 (Fig. 4.8, Fig. 4.4H). Percentage cover of bare rock did not change significantly over time in any of the density treatments (Table 4.11, Fig. 4.8).

**Table 4.11**. Results of a three-way Repeated Measures ANOVA on the effects of site, density and time (and their interactions) on the percentage cover of bare rock. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| Site | 1 | 33606 | 33606 | 75.146 | <0.001* |
| Density | 3 | 126171 | 42057 | 3.026 | 0.071 |
| Time | 12 | 4943 | 412 | 0.921 | 0.526 |
| Site: Density | 3 | 36912 | 12304 | 27.513 | <0.001* |
| Site: Time | 12 | 2720 | 227 | 0.507 | 0.910 |
| Density: Time | 36 | 8690 | 241 | 0.540 | 0.986 |
| Site: Density: Time | 36 | 9673 | 269 | 0.601 | 0.967 |
| Residuals | 300 | 134163 | 447 | | |

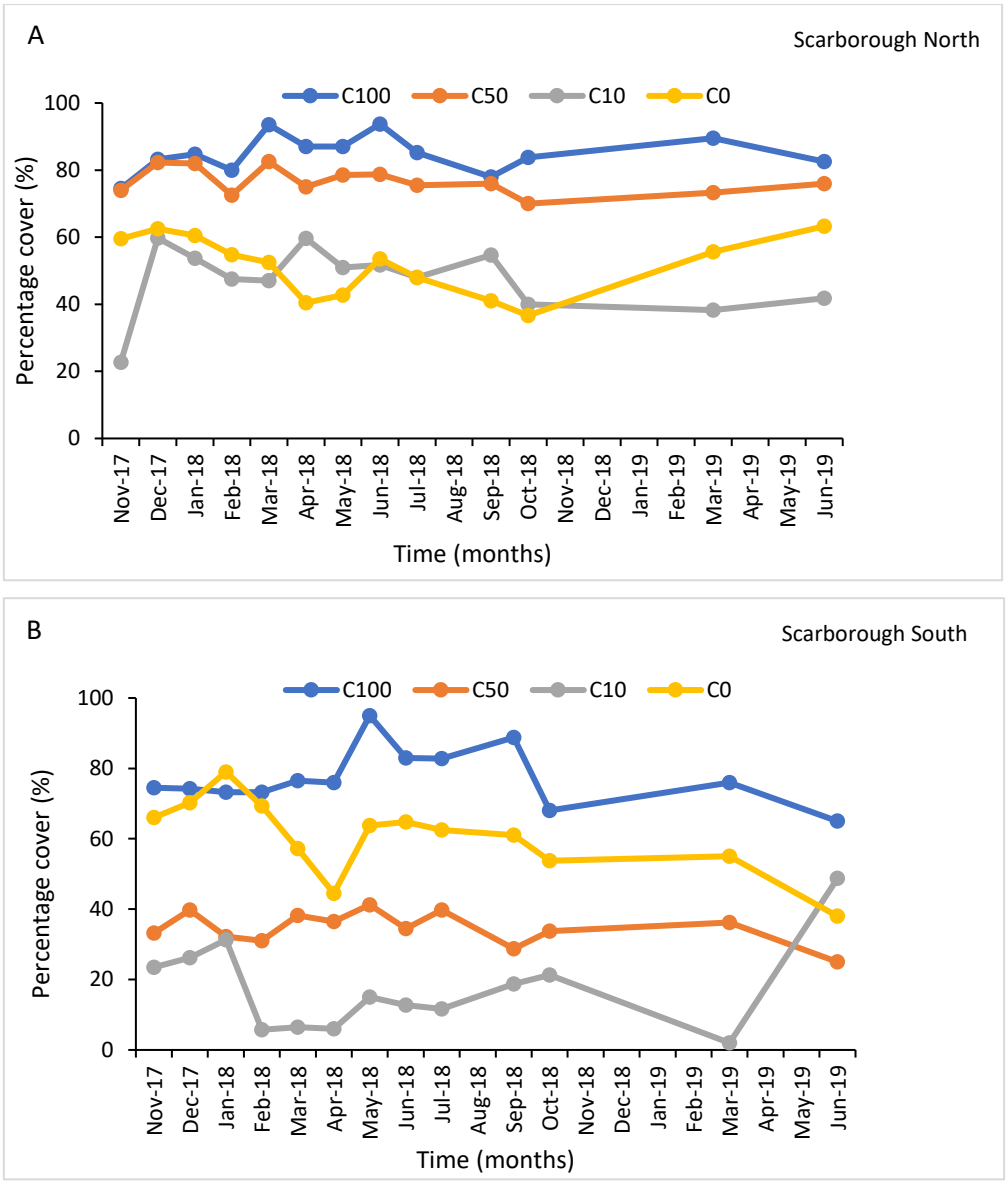



Figure 4.8. Percentage cover of bare rock with regard to limpet densities over time in two sites. See caption to Fig. 4.5 for further details.

*Limpet recruitment*

A three-way Repeated Measures ANOVA of the densities of recruits of *C. granatina* revealed a significant main effect of time, and an interactive effect of site and density, which indicated that the effects of removing *C. granatina* on its own recruits differed between sites (Table 4.12). Recruitment was high in January and February of the first year and reached a peak in Jan 2018, which was the only time when there was a significant difference of limpet recruits among experimental adult densities (Fig, 4.9), suggesting that recruitment variability was driven by season and not adult densities.

**Table 4.12**. Results of a three-way Repeated Measures ANOVA on the effects of site, density and time (as well as their interactions) on the density of recruits. Asterisks indicate significant effects.

| Source | Df | SS | MS | Pseudo-F | P(perm) |
|---|---|---|---|---|---|
| Site | 1 | 87.7 | 87.69 | 11.424 | <0.001* |
| Density | 3 | 148.4 | 49.46 | 3.634 | 0.045* |
| Time | 12 | 426.6 | 35.55 | 4.631 | <0.001* |
| Site: Density | 3 | 79.4 | 26.48 | 3.450 | 0.017* |
| Site: Time | 12 | 144.0 | 12.00 | 1.564 | 0.101 |
| Density: Time | 36 | 360.5 | 10.01 | 1.305 | 0.122 |
| Site: Density: Time | 36 | 260.2 | 7.23 | 0.942 | 0.569 |
| Residuals | 300 | 2302.9 | 7.68 | | |

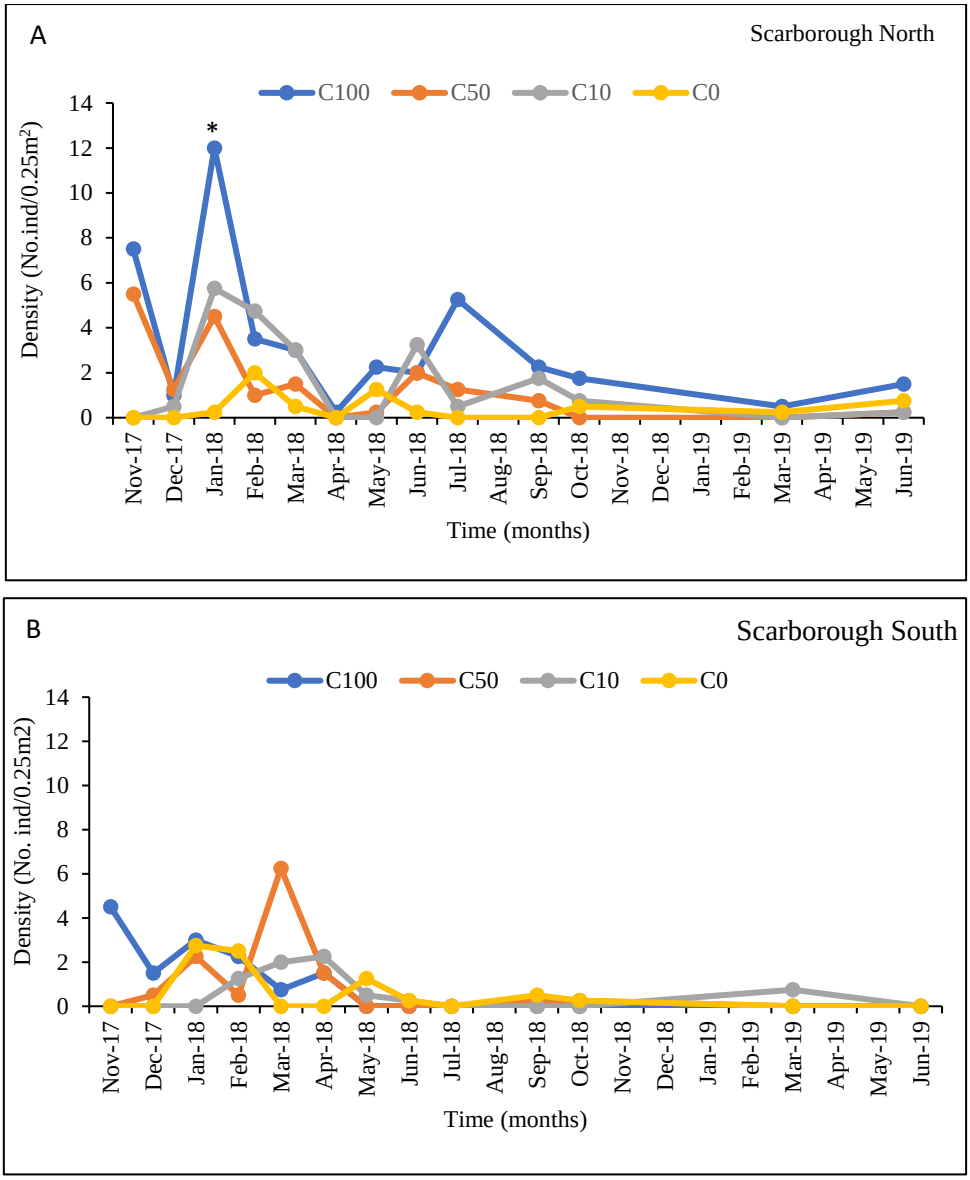



Figure 4.9. Mean densities of *Cymbula granatina* recruits in relation to the densities of adults, plotted over time at Scarborough North (A) and Scarborough South (B). C100, C50, C10 and C0 respectively represent densities in caged plots of 100% (control plots with no reduction) and reductions to levels of 50%, 10% and 0%. The only instance where pairwise posthoc comparisons confirmed a significant effect of adult densities on recruits is indicated by the asterisk in (A) for January 2018.

*Relationships between C. granatina abundances and different functional groups*

Pooling the data for both sites, quantile regressions showed that there was a significant negative relationship between the abundance of *C. granatina* and the percentage covers of corticated, encrusting and ephemeral algae except for the quantile levels 0.1-0.3 for corticated, 0.1-0.5 for ephemeral, and 0.1-0.2 for encrusting algae (Table 4.13, Fig. 4.10A-C). However, grazer abundance displayed no significant relationship with *C. granatina* abundance, despite an apparent decline in their abundance at higher level of *C. granatina cover* (Table 4.13, Fig. 4.10D).

**Table 4.13.** Coefficients and p-values for the relationship between *C. granatina* densities and various functional groups across different quantile levels.

| | Quantile level | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 |
| Corticated algae | | | | | | | | | |
| P-value | 1.000 | 1.000 | 0.330 | 0.019 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Coefficients | 0.000 | 0.000 | -0.036 | -0.094 | -0.158 | -0.278 | -0.426 | -0.786 | -0.875 |
| Ephemeral algae | | | | | | | | | |
| P-value | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Coefficients | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | -0.020 | -0.023 | -0.040 | -0.089 |
| Encrusting algae | | | | | | | | | |
| P-value | 0.819 | 0.064 | 0.005 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Coefficients | -0.022 | -0.222 | -0.393 | -0.500 | -0.688 | -0.964 | -1.389 | -1.250 | -0.750 |
| Grazers | | | | | | | | | |
| P-value | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| Coefficients | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

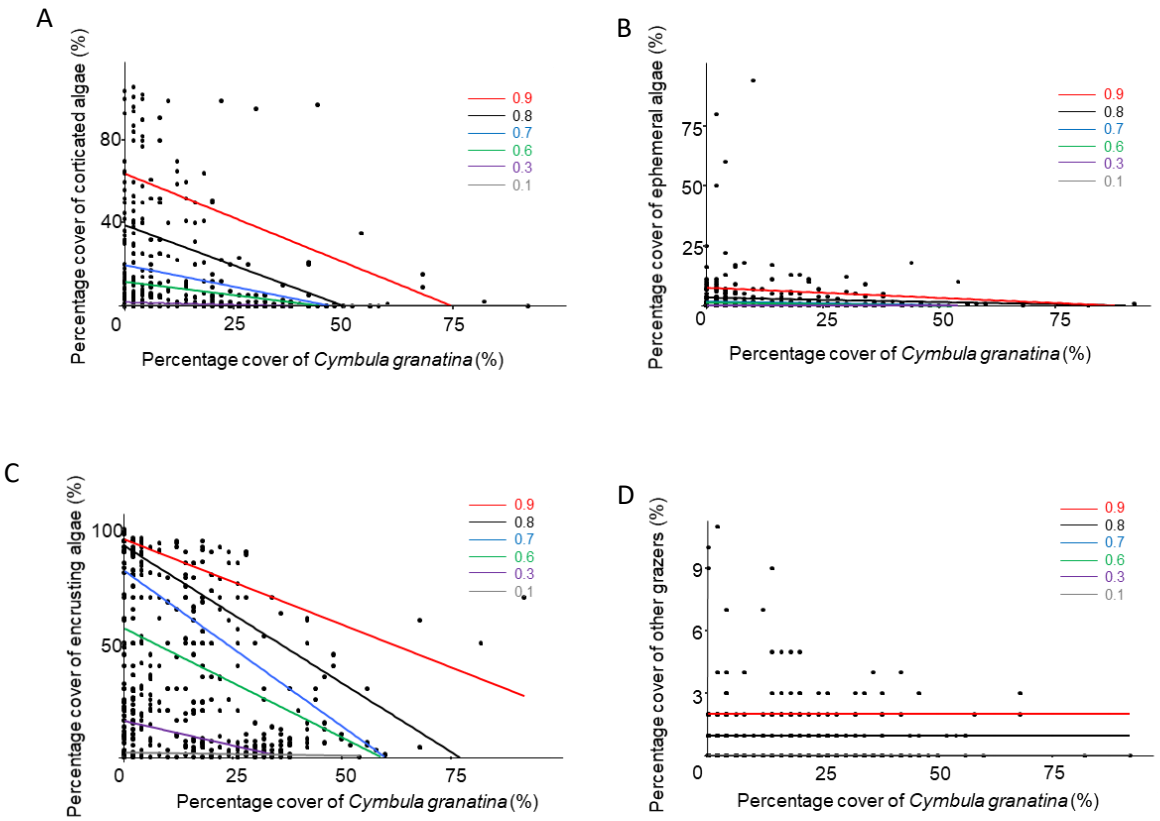



Figure 4.10 Relationships between the percentage cover of *C. granatina* and that of corticated, ephemeral and encrusting algae, and grazers. Because of the wedge-shaped distribution of data, quantile regressions were used to meet regression assumptions. Lines show estimated regression quantile functions.

# Discussion

*Effects of limpet removal on community composition*

This study assessed the impacts of removing or thinning the density of the limpet *Cymbula granatina* on the community composition of rocky shore organisms at two sites in the Table Mountain National Park Marine Protected Area. As predicted, the removal or substantial reductions of the density of *C. granatina* led to overall changes in community composition, but the responses to different density manipulations differed between the sites. The impacts of limpet removal on community composition also varied over time, with natural seasonal variability in algal cover, in particular, taking place. Removal of limpets resulted in increases in percentage cover of corticated algae and ephemeral algae as expected, but crustose algae were influenced in a manner that was site-specific, being reduced by high limpet densities at Scarborough North but peaking at intermediate limpet densities at Scarborough South. Of the other functional groups, grazers and recruits of *C. granatina* were unaffected by the different experimental harvesting regimes, and filter feeders (other than mussels) were affected minimally.

Exclusion of limpets from rocky shores is known to cause dramatic changes in community composition (Dye 1995, Maneveldt et al. 2009, Martins et al. 2010b). These differences are mostly associated with a substantial increase in macroalgal cover in areas when grazing pressure is reduced (Farrell 1988, Dye 1993, 1995, Maneveldt et al. 2009, Martins et al. 2010b, Aguilera & Navarrete 2012, Aguilera et al. 2015). In addition, areas where limpets are thinned or removed may become colonised by mussels such as *Mytilus galloprovincialis*, barnacles and other limpet species as a result of reduced competition for space and food (Eekhout et al. 1992, Dye 1993, 1995, Lindberg et al. 1998, Maneveldt et al. 2009, Borges et al. 2015, Tejada-Martinez et al. 2016, Ellrich et al. 2020). In my study, removal of *C. granatina* resulted in changes in community composition in the low-density (high harvesting) regimes, mainly due to increased percentage cover of corticated and ephemeral algae. High-density control plots contained large amounts of bare rock but, interestingly, complete removal of limpets at Scarborough South led to the second-highest prevalence of bare rock, indicating that a low abundance (rather than complete absence) of limpets has the potential to generate space for colonisation of rocky shores by algae. My overall results showing proliferation of macroalgae

in plots with low- or zero-densities of limpets are in agreement with earlier findings on the South African east coast and elsewhere (Dye 1993, 1995, Maneveldt et al. 2009, Aguilera & Navarrete 2012, Aguilera et al. 2015). Surprisingly, only on one occasion did complete removal of *C. granatina* in the zero-density treatment result in a significant difference in community composition from the plots with maximal limpet densities. This is counter-intuitive, as most other studies have shown greatest developments of algae following complete removal of limpets (Dye 1993, 1995, Maneveldt et al. 2009, Martins et al. 2010b, Aguilera & Navarrete 2012, Aguilera et al. 2015). Low algal growth in the complete-removal plots was also unexpected because the region is highly productive as a result of nutrient injections by upwelling (Bustamante et al. 1995b, Robinson et al. 2008). However, many studies have shown that limpets fertilize algae and promote their growth (Branch 1976, Plagányi & Branch 2000; Maneveldt et al. 2006). This occurs partly because limpets excrete ammonium, nitrate and urea, but also beacuse their mucus contains nutrients that enhance algal growth (Clarke 1990, McQquaid & Froneman 1993, Suda et al. 2015). This mucus is usually found under the feet of the limpets or on trails that they leave as they forage. Thus, removal of limpets might have reduced the nutrient availability to algae to the point of limiting growth. Nonetheless, the fact that a 90% removal of *C. granatina* individuals led to altered community composition at both sites indicates that in terms of ecosystem effects, sustainable harvesting levels should be held below that level. My experimental reduction of limpet densities by 50% only once yielded a significant difference in community composition from the natural (i.e. 100%) density treatment, implying that thinning limpets down to that level will have relatively few ecosystem effects.

*Effects of limpet removal on the percentage cover of algae*

Grazing by limpets limits algal colonisation and reduces their abundance on intertidal rocky shores (Luckens 1974, Benedetti-Cecchi et al. 1996, 2001, Boaventura et al. 2002, Jenkins et al. 2005, Coleman et al. 2006, Phillips & Hutchison 2008, Martins et al. 2010b, Barbiero et al. 2011, Connor et al. 2011, Crowe et al. 2011, Borges et al. 2015, 2016). Macroalgae proliferate in areas where limpets are removed because of the reduction in grazing pressure (Benedetti-Cecchi et al. 2001, Boaventura et al. 2002, Barbiero et al. 2011). In accord with these findings, my study showed that corticated and ephemeral algae flourished in exclusion cages with few or no limpets.

The abundance of ephemeral algae such as *Ulva* spp. was generally low in all treatments (below 5% cover). This group is known to constitute up to 42% of the diet of *C. granatina* (Bustamante et al. 1995a). Thus, the low abundances of ephemeral algae in low-density limpet plots was unexpected, as ephemeral algae usually flourish in the absence of limpets (Dye 1995, Lasiak & Field 1995, Lasiak 1998, 1999, Benedetti-Cecchi et al. 2001, Lindegarth et al. 2001, Phillips & Hutchison 2008, Maneveldt et al. 2009, Babcock et al. 2010, Aguilera & Navarrete 2012, Deepananda & Macusi 2012, Tejada-Martinez et al. 2016). However, when the months of greatest ephemeral algal abundance (January to May 2018) were considered in isolation, it was evident that they reached highest abundance in the two treatments with lowest limpet abundances. Conversely, the absence of any limpet-density effect in times when the algae were scarce infers that influences other than grazing are controlling their abundance at such times, possibly related to a reduction in nutrient and light supplies when upwelling diminishes in the cooler months of the year as upwelling-favourable winds decline (Andrews & Hutchings 1980, Shannon 1985).

In addition to the effects of grazing, Benedetti-Cecchi et al. (2001) and Guerry & Menge (2017) have reported that in areas with high nutrient availability – as is the case in the Southern Benguela upwelling region where my study was done – algae and limpets tend to compete for space. Thus, removal of limpets not only reduces grazing pressure but also lessens competition for space, boosting recruitment of algae on the bare rock vacated by limpets. Surprisingly, encrusting algal cover did not change significantly over time and their abundance was low in the control plots with the highest limpet densities and high in the two treatment with low to zero densities. My hypothesis that these algae would increase in the high-density plots because they are grazer-resistant and benefit from grazing that prevents their overgrowth by erect algae was thus rejected. This contradicts multiple earlier findings on the relationship between limpets and encrusting algae (Branch 1976, Steneck 1982, Farrell 1988, Keats et al. 1994, Benedetti-Cecchi et al. 1996, 2001, Plagányi & Branch 2000, Bulleri et al. 2000, Maneveldt et al. 2006, Maneveldt & Keats 2008, Blamey & Branch 2009, Martins et al. 2010b, Aguilera & Navarrete 2012, Aguilera et al. 2015, Guerry & Menge 2017, Daza-Guerra et al. 2020). The reason my outcome departed from that predicted by this body of research remains unknown. It is possible that differences in crustose cover among different limpet densities existed at the start of the experiment and were simply perpetuated over the course of the experiment because crustose algae grow slowly (Steneck 1986, Steneck & Dethier 1994, Dethier & Steneck 2001, Maneveldt & Keats 2008), and may not have had sufficient time to respond to differences in

grazing intensity. This stands in strong contrast to the corticated and ephemeral algae, both of which occurred at uniformly low abundances at the start of the experiment, but rapidly diverged to develop high levels of cover in plots with low or zero densities of limpets while remaining at low levels in high-density plots – an unambiguous response to reduced grazing.

The interaction between limpets and macroalgae is, however, not all one-way traffic. Underwood & Jernakoff (1981) showed that in New South Wales, Australia, macroalgae grow prolifically low on the shore and are capable of excluding grazers such as the limpet *Cellana tramoserica* because they occupy hard-rock space and restrict access to substratum on which the limpets graze microalgae and sporelings.

*Effects of limpet removal on the abundance of grazers*

Interspecific competition exists among grazers for food and may lead to reduced body mass, elimination or mortality of inferior competitors. Conversely, they may increase in numbers after removal of a dominant competitor (Branch & Branch 1980, Branch 1984, Dye 1993, 1995, Maneveldt et al. 2009, Martins et al. 2010b). For example, Maneveldt et al. (2009) reported increases in the abundance of the limpets *Scutellastra longicosta* and *Siphonaria capensis* following the removal of another limpet, *Cymbula oculus*. Dye (1993) reported an increase in the abundance of other grazers following removal of limpets in Transkei, South Africa; and in southern California, removal of the territorial giant limpet *Lottia gigantea* was followed by an incursion of smaller species of limpets (Lindberg et al. 1988). However, in my study, grazer abundance remained low in the exclusion plots and did not increase over time. This contradicts the previous findings which showed increases in the abundance of grazers following removal of limpets (Dye 1993, 1995, Maneveldt et al. 2009, Martins et al. 2010b). This may be due to the fact that *C. granatina* creates dense beds, excluding most other grazers (Bustamante et al. 1995a), so there were few other grazers in the vicinity to move into plots from where *C. granatina* was thinned or removed. Dye (1995) found that at one of his experimental sites, Dwesa on the south-east coast of South Africa, limpets and other grazers rapidly moved into cleared plots and influenced the development of algae, whereas at a second nearby site, Nqabara, this did not occur. He attributed this difference to low grazer densities at Nqabara. The same principle likely applies in my study, as grazer abundance was generally low in *C. granatina* beds.

*Effects of limpet removal on limpet recruitment*

Patellid limpets tend to recruit most intensively in areas where adult densities are low (Underwood et al. 1983, Farrell 1988, Delany et al. 1998, Branch & Odendaal 2003, Nakin & McQuaid 2016) because of mortality of recruits caused by adult bulldozing and grazing (Delany et al. 1998, Nakin & McQuaid 2016). This is, however, not the case for all limpet species. *Scutellastra cochlear* recruits in greatest amounts where its adults are concentrated (Branch 1975c), despite the fact that adults do graze on recruits (Branch 1981). My results tend to contradict the prevailing view that limpet recruitment is generally reduced where adults are abundant, for the lowest densities of *C. granatina* recruits were mostly found on the zero-density plots where adults were absent, and peak values were located in plots with either maximum densities or 50% reduction. However, the numbers recorded were low and variable, and differences in the effects of adult density existed between the sites; so the results should be treated with circumspection. Nevertheless, my findings support those of Eekhout et al. (1992) who also noticed reduced recruitment of *C. granatina* in areas where this species was harvested experimentally. This could be associated with recruits settling on the shells of adults of *C. granatina* and therefore incidentally being removed when adults are harvested (Eekhout et al. 1992). Use of the shells of adults as settlement areas for recruits has also been reported in the Agulhas ecoregion for *Cymbula oculus* (Maneveldt et al. 2009) and *Scutellastra cochlear* (Branch 1975b, c), which accords with the findings of Kay (2002) that high densities of larval settlement of *Lottia digitalis* occur in areas with high adult densities.

*Effects of limpet removal on the on percentage cover of bare rock*

Grazing by limpets at high densities often reduces algal abundance and prevents colonisation of bare rock because they feed on the propagules of algae, increasing the amount of bare rock (Farrell 1988, Dye 1995, Maneveldt et al. 2009, Martins et al. 2010b, Aguilera & Navarrete 2012, Aguilera et al. 2015). Conversely, exclusion of grazers reduces bare rock due to an increase in algal cover (Maneveldt et al. 2009, Martins et al. 2010b, Aguilera & Navarrete 2012, Aguilera et al. 2015). My study was in accord with this: highest incidences of bare rock occurred in the natural-density plots from which no limpets were removed. The lowest incidence of bare rock occurred in the two low-density plots at Scarborough North but, curiously, at Scarborough South the second-highest values for bare space were found in the

zero-density plots, suggesting that factors other than grazing disturb some rocky-shore communities, such as sand scouring, desiccation or smothering by other organisms. The high bare-rock values under natural (100%) limpet densities were associated with consistently low abundances of corticated and ephemeral algae. The high average bare rock cover of 85% that I recorded in control plots is in line with the findings of other studies (Martins et al. 2010b, Aguilera et al. 2015).

## Conclusions

Removal of all or more than half the *C. granatina* led to changes in community composition, upholding my first hypothesis that community composition would change following limpet thinning and that the effect would be related to the magnitude of the thinning.

More specifically, reducing limpet densities led to increases in the cover of corticated and ephemeral algae as a response to reduced grazing pressure, and varied with the extent to which the limpets were thinned, as predicted. The magnitude of the effect was, however, also influenced by seasonal changes in the abundance of these algal groups, and their responses to limpet thinning were only measurable during months when these algae were most prolific, which corresponded with the upwelling season. Because of this seasonal effect, community composition tended to be cyclical, returning close to its starting point on a roughly annual basis. Nevertheless, the trajectories followed by the paths of plots for the four different density treatments emerged as being distinctively different. Collectively, this upholds my second hypothesis that corticated and ephemeral algae would increase in proportion to the extent to which *C. granatina* was thinned.

Encrusting algae on the other hand did not respond to the removal of *C. granatina* in a manner corresponding to my hypothesis that they would reach greatest cover at high limpet densities – thus contradicting my third hypothesis. Indeed, highest cover was reached in zero-density plots and lowest cover in the highest-density plots. There was no temporal change in encrusting algae, and it is possible that the percentage cover recorded for encrusting algae is just a reflection of their staring abundances, rather than responses to limpet densities.

My fourth hypothesis, that recruitment of *C. granatina* would increase as adults were thinned,

was rejected as recruits were most abundant on the control plots with maximal densities, thus showing a positive association with adult density. This has management implications as adults are preferentially removed in the harvested areas of the MPA, and recruits might be accidentally removed. I am, however, cautious of attaching too much significance to this outcome, as the numbers of recruits were low. Finally, and unexpectedly, other grazers did not invade the plots where *C. granatina* was thinned or removed, thus refuting my fifth hypothesis.

Clearly, harvesting of *C. granatina* has the potential to change community composition substantially. On sheltered shores where there is no human harvesting, *C. granatina* can attain considerable densities, and its biomass on low-to-mid intertidal zones of embayments can achieve levels second only to those of *Scutellastra argenvillei*, which itself has the highest biomass recorded for any intertidal grazer in the world (Bustamante et al. 1995a). This emphasises the potential magnitude of harvesting impacts on rocky shores dominated by *C. granatina*, which – as I have shown - completely changes community composition.

There is, however, a wrinkle to this story, for *C. granatina* attains its high densities and biomasses only because it acts as a 'trapper', trapping drift kelp and other seaweeds beneath its foot when algal debris accumulates in sheltered bays (Bustamante et al. 1995a, Bustamante & Branch 1996b). The consequence of this is that the effects of *C. granatina* on living algae attached to the rocks is muted. Adults of *C. granatina* feed virtually exclusively on drift algae. Juveniles < 40 mm shell length cannot feed this way and subsist largely on diatoms, microalgae and the sporelings of macroalgae (Bustamante & Branch, 1996b), and it is they that are most likely to influence the growth of algae on the shore. Most experiments involving the removal of limpets from the shore record rapid responses and decisive changes to a situation dominated by algae (e.g., Jones 1946, Lodge 1948, Hawkins & Hartnoll 1983, Steffani & Branch 2003, 2005, Jenkins et al. 2005, Branch et al. 2008, 2010, Maneveldt et al. 2009, Crowe et al. 2011, Borges et al. 2015). By comparison, the responses I recorded were slow, only emerged when algae displayed season peaks in abundance, and did not extend to encrusting algae or influence other grazers. Much of this may be attributed to the fact that only the juveniles of *C. granatina* are likely to be affecting community composition by grazing on the young stages of algae rather than trapping drift algae.

# Chapter 5: General conclusions

Marine Protected Areas (MPAs) worldwide have among their objectives the protection of biodiversity, provision of refugia for endangered, vulnerable and exploited species, and a recovery of populations that will improve their conservation status (Durán & Castilla 1989, Hockey & Branch 1997, Babcock et al. 1999, 2010, Shears & Babcock 2002, Micheli et al. 2004, Parnell et al. 2005, Guidetti 2007, Guidetti & Sala 2007, Maneveldt et al. 2009, Coppa et al. 2012, Baskett & Barnett 2015, Sala & Giakoumi 2018). These objectives are achieved primarily by reducing human harvesting pressure and other disturbances (Hockey & Branch 1997, Holt & Stewart 2012), by setting up no-take areas and regulating harvested zones within MPAs (Coppa et al. 2012, 2015). The effectiveness of no-take areas depends greatly on the effective implementation of legislation and on compliance (Agardy et al. 2011); if compliance is low, protection of populations is not guaranteed even in no-take MPAs (van Herwerden et al. 1989, Coppa et al. 2012, 2015). Effectiveness is also related to the sizes and ages of MPAs, with larger and older MPAs being more effective (Claudet et al. 2008, Ban et al. 2019, McClanahan et al. 2020).

My study focused on evaluating the role of Table Mountain National Park MPA (TMNP MPA) as a conservation tool for intertidal biodiversity. More specifically, I compared 'no-take' restricted zones in the park with those classed as 'controlled', where harvesting takes place within the limits of national laws. To determine the relative efficacy of these conservation tools, I adopted three approaches. Firstly, in Chapter 2 I used a control-impact approach to compare community composition and the densities and sizes of commonly harvested and rarely harvested limpets among 16 sites representing the two protection levels of the MPA. In this context, I tested four hypothesis to provide insights into whether the no-take sections of the MPA perform their role of maintaining communities in a natural state, and sustain larger populations and sizes of commonly harvested species than in 'controlled' zones of the MPA.

In Chapter 3 I went into more detail at a subset of the sites and focused on a second aspect, namely a before-after-control-impact comparison using historical data from 1970 and modern data from 2017 that were collected in the same fashion. Against this historical baseline, I evaluated temporal changes and spatial differences in community composition and the densities and sizes of commonly and rarely harvested limpets, in relation to increased harvesting

pressure and the arrival and spread of the alien invasive Mediterranean mussel *M. galloprovincialis*, which were the major anthropogenic changes affecting rocky shores in the past four decades. In addition, Chapter 3 also evaluated the effects of protection by studying changes in the density, sizes and communities between two harvested sites and two others that have been protected from harvesting by the TMNP MPA. The arrival of *Mytilus galloprovincialis* transformed the mid-shore zones, excluding adults of the granular limpet *Scutellastra granularis*, although juveniles benefit from the mussel by finding a secondary home on the shells of the mussel. I also found that harvesting has decimated the granite limpet *Cymbula granatina* and Argenville's limpet *Scutellastra argenvillei*, leading to a proliferation of opportunistic seaweeds, such as *Ulva* spp., and corticated algae, notably *Pachymenia orbitosa*.

As outlined in Chapter 4, my third approach was a field-based experimental test to evaluate the effects of removing or thinning the commonly harvested limpet and key grazer *Cymbula granatina* on rock- shore community composition. This chapter allowed an assessment of the level at which harvesting of *C. granatina* is sustainable. I found that following removal or substantial thinning of *C. granatina*, community composition changed, cover of corticated and ephemeral algae increased and recruitment of *C. granatina* decreased. However, these effects were dependent on the proportions of *C. granatina* removed, with thinning down to 50% of natural densities having few effects. These outcomes are important for evaluating the effectiveness of the TMNP MPA and in informing sustainable utilization of resources and adaptive management of this MPA.

This final synoptic chapter deals with conservation implications of the findings of chapters 2-4. Firstly, the higher abundances of limpets *Cymbula granatina*, *Cymbula oculus* and *Scutellastra argenvillei* in the no-take areas (Chapter 2) and their reduced densities in the harvested areas are evidence that the no-take areas of the TMNP MPA meet the objective of maintaining naturally high population levels. For mobile groups, when populations are healthy and abundant in no-take areas, migration may take place to adjacent harvested areas due to competition, leading to improved yields in depleted stocks through adult spill over (García-Charton et al. 2008, Lester & Halpern 2008, Cole et al. 2011, Fenberg et al. 2012, Buxton et al. 2014). For example, it has been shown that the Columbretes Reserve off the west coast of Spain contributes 31–43% to the spill over of lobsters (Fenberg et al. 2012). However, outcomes such as this depend on the movement and dispersal capabilities of the exploited

species involved, and adults of groups such as limpets and mussels do not move long distances (Cole et al. 2011, Alexander & Gladstone 2012). In such cases, colonisation of fished grounds will depend largely on the exportation of larvae. So, for example, Pelc et al. (2009) demonstrated that larval dispersal from no-take MPAs on the south-east coast of South Africa boosted populations of the mussel *Perna perna* outside the MPA boundaries.

Another role attributed to MPAs is that they maintain greater abundances and sizes of breeding individuals, especially for populations that are susceptible to harvesting (Hockey & Branch 1997, Cole et al. 2011). In Chapter 2, I showed that sizes of commonly harvested limpets were larger in the no-take areas of the TMNP MPA. These large individuals will have a high reproductive output as a result of fecundity increasing with age and size (Pelc et al. 2009, Alexander & Gladstone 2012). In relation to fish, this has been developed as the BOFFFF hypothesis (Big Old Fat Fecund Female Fish), that large individuals contribute disproportionately to reproductive output (Berkeley et al. 2004). Populations in MPAs that sustain large individuals therefore become a source of larvae that can subsidize adjacent harvested areas (Agardy 1994, Branch & Odendaal 2003, Pelc et al. 2009, Cole et al. 2011, Alexander & Gladstone 2012). The higher abundances of large *C. granatina* and *S. argenvillei* in the no-take sections of the TMNP indicate protection of adult limpets, which will influence recruitment directly by the production of large amounts of larvae that can be exported, and indirectly as recruits of both these species and other taxa preferably settle on the shells of adults (Eekhout et al. 1992, Pelc et al. 2009, Cole et al. 2011, Buxton et al. 2014). This important contribution of MPAs goes beyond their boundaries, leading to improved productivity of fisheries. My study did not cover settlement, and only touched on recruitment. Thus, future studies should be devoted to the settlement and recruitment patterns between zones with different protection levels, and even beyond the bounds of the MPA, to better understand the role of the MPA in replenishing populations in harvested areas.

While some of the patterns emerging from my data yielded clear-cut evidence of the efficacy of no-take MPAs, with larger sizes and greater densities of harvested species being recorded in no-take areas, there were ambiguities, such as the larger sizes of *Cymbula oculus* in some harvested areas relative to no-take areas, and the greater abundances of algae in some no-take areas that were expected to support lower abundances due to greater grazing pressure there. The apparent effectiveness of MPAs will be influenced not only by the level of compliance to regulations, coupled with the efficiency of surveillance (Giakoumi et al 2018), but also the

magnitude of harvesting taking place, both outside and inside MPAs (Barrett et al. 2007, Nakin & McQuaid 2014), which can in reality vary substantially between areas that are assigned the same protection level on paper. I did not have any quantitative data on the degree of exploitation and compliance to regulations at my study sites, and had to rely on a ranking of sites based on expert opinion to assess whether harvesting intensity influenced the outcomes. Quantitative data on the degrees of exploitation and compliance would help in assessing the efficacy of no-take versus harvested areas, assist planning of daily law-enforcement operations to prioritise areas that are heavily used, and identify times and areas where compliance is low. This information is important since the effectiveness of this MPA depends on the extent to which harvesting takes place and whether law enforcement is sufficient to ensure compliance with regulations.

My study demonstrated that harvesting in the harvested areas altered rocky-shore community composition, which differed from that in no-take areas. This indicates that protection does allow recovery or maintenance of natural ecosystem functioning in the no-take areas and, conversely, that harvesting significantly alters the ecosystem state and functioning. Where harvesting was absent or minimal, communities were dominated by filter feeders, trappers and grazers, which shows that protection strengthens ecological processes such as grazing, predation, competition and recruitment, and results in natural top-down and bottom-up effects that maintain community composition (Moreno et al. 1986, Agardy 1994, Hockey & Branch 1997, Benedetti-Cecchi et al. 2003a, Shears & Babcock 2003, Micheli et al. 2005, O'Sullivan & Emmerson 2011, Alexander & Gladstone 2012, Fenberg et al. 2012, Leleu et al. 2012). These ecological processes are reduced in harvested areas as result of the depletion of filter feeders and benthic herbivores, leading to dominance of algae, which compete with sessile organisms for space. High abundances of algae inhibit settlement of sessile organisms, smother organisms through overgrowth, and reduce feeding by micro-algal grazers (Lasiak & Field 1995, Lasiak 1998). These effects slow recovery of populations and hinder the colonisation of harvested areas by sessile organisms.

The data analysed in chapter 2 also provide a baseline from which a monitoring programme for rocky shores can be established to further evaluate MPA effects in the TMNP MPA, and to assess any shifts due to climate change or alien invasions. The design of the monitoring programme should consider rock type and biogeographic region and, within in each biogeographic region, a minimum of four sites (two harvested and two no-take areas with each

protection level being represented by replicates of the two main rock types). This information will be valuable for implementing a long-term marine monitoring programme for the TMNP MPA, which has thus far not been done. Rocky shores are very accessible and therefore particularly vulnerable to human impacts, but are relatively easy to monitor; the establishment of benthic monitoring in the intertidal zone is thus cost-efficient and logistically more feasible than equivalent sub-tidal monitoring. It is therefore strongly recommended that the baseline information generated in this study should be used to design an appropriate marine monitoring programme for this MPA.

In chapter 3, I showed that the arrival and spread of *M. galloprovincialis* has affected biodiversity patterns, by displacing indigenous species and altering community composition, as well as by changing the ontogenetic zonation patterns of species such as *Scutellastra granularis*. The presence of *M. galloprovincialis* in the no-take areas thus jeopardises their role of preserving biodiversity in a natural state. Given the fact that alien species on the South African shores are increasing, and that the TMNP MPA is situated in an area with heavy shipping traffic, the MPA is susceptible to further species introductions, which cannot be halted solely by the existence of the MPA. If effectively implemented and managed, MPAs can be successful in controlling human harvesting, but they are powerless to counter alien arrivals that have broadly dispersing larvae. There is a need for an international alien monitoring programme that should prioritise MPAs to ensure early detection to improve the chances of eradication of alien species before they become established and spread.

The comparisons with historical data in my study demonstrated that intensified harvesting has reduced densities and sizes of commonly harvested limpets, and altered community composition at harvested sites. The establishment of no-take areas in the TMNP MPA has reduced harvesting there, as indicated by greater densities and sizes and more naturally composed and functioning ecosystems. The increase in harvesting pressure is linked with an increase in the human population along the coast, coupled with an increase in poverty associated with high unemployment rates and inadequate education provided in poor neighbourhoods. The intensification of harvesting is a major threat to the biodiversity, as natural resources become an accessible alternative source of protein that consumed by the growing coastal communities. As poverty and coastal settlements grow, enforcement of conservation regulations becomes difficult and increased poaching activities along the coast exert pressure on the biodiversity. Thus, an effective surveillance and law enforcement system

throughout the MPA is essential to ensure that resource users comply with the regulations set by the Marine Living Resource Act of 1998. There is, however, a need for a study that will assess the actual patterns and intensities of harvesting in and around the MPA, as this information will improve understanding of the organisms that are collected, the rates at which they are collected, the number of people harvesting, the areas that experience intense harvesting and the times when harvesting is high. Lastly, there is a need to consult with and consider the needs of local communities when planning MPAs (Dehens & Fanning 2018, Sowman et al. 2011), and to educate resource users about the importance of adhering to regulations (Ferreira 2011). These overarching principles extend beyond the reach of my thesis, but their importance should not be underestimated.

In chapter 4, I showed that removal of all or more than half of the natural population levels of *C. granatina* led to changes in community composition, with ephemeral and corticated algae dominating. This has management implications as *C. granatina* is intensely harvested along the west coast of the Cape Peninsula (see Chapter 2) and its densities have already declined by over 50% at harvested sites (see Chapter 3). Reduced populations may lead to low recruitment. Thus, the intensity with which this species is harvested needs to be evaluated to ensure that harvesting is sustainable and has no ecosystem effects. There is also a need to study the factors influencing recruitment of this species to ensure the persistence of its populations.

The comparisons on which these conclusions rest were based solely on no-take (restricted) areas versus partially protected (controlled) areas within the overall umbrella of the Table Mountain National Park MPA, so the differences that transpired reflect the fact that full protection is more beneficial for biodiversity conservation than partial protection, as others have shown elsewhere (Currie et al. 2012, Floros et al. 2013, Giakoumi et al. 2017, Harasti et al. 2018). The scope of my work did not allow me to assess whether the partial protection granted in 'controlled' zones is any more (or less) effective than in areas beyond the park, which are subject to the same regulations. For such an assessment, an expanded programme would need to make comparisons with harvested shores falling outside the TMNP MPA.

## Chapter 6: References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